ESTIMATION OF GENETIC PARAMETERS FOR FERTILITY TRAITS AND THE EFFECT OF MILK PRODUCTION ON REPRODUCTION PERFORMANCE IN SOUTH AFRICAN HOLSTEIN COWS

by

Johannes Phillipus Potgieter

Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Agriculture (Animal Science)

at

Stellenbosch University

Department of Animal Sciences

Faculty of AgriScience

Supervisor: Prof K Dzama

Date: March 2012

Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated) the reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: March 2012

Abstract

Estimation of genetic parameters for fertility traits and the effect of milk production on reproduction performance in South African Holstein

Candidate	**:**	**Johan Potgieter**
Study leader	**:**	**Professor K. Dzama**
Department	**:**	**Animal Sciences**
Faculty	**:**	**AgriSciences**
Degree	**:**	**MSc (Agric)**

Profitable milk production and genetic improvement in dairy herds are largely dependant on fertile cows capable of calving down on an annual basis. Several studies indicate declines in the reproductive performance of Holstein cows over the last 30 years. Calving interval (CI) and services per conception (SPC) are being used by dairy farmers as indicators of the reproductive performance of dairy cows. However, using these traits as cow fertility indicators is problematic as CI is dependent on subsequent calving dates while SPC is strongly linked to inseminator proficiency. The aim of the study is therefore, firstly, to describe alternative fertility traits derived from insemination and calving dates and pregnancy check results. The effects of some non-genetic factors on these traits are discussed. Means±sd for interval traits from calving to first insemination (CFS) and the interval from calving to conception (DO) were respectively 77±30 and 134±74 days while the number of services per conception (SPC) averaged 2.55±1.79. The percentage of first servics occurring within 80 days post-partum (FS80d) and the proportion of cows being confirmed pregnant within 100 (PD100d) and 200 days post-partum (PD200d) were 0.64±0.48, 0.36±0.48 and 0.71±0.45, respectively. Although fertility traits were affected significantly by lactation number, calving year and month, herds (managers) had the largest effect.

Fertility is a complex trait, however, the challenge is finding traits that best describe this trait. Genetic parameters for these traits could give an indication of the response to selection in dairy herds. In the second part of this study, genetic parameters and correlations between fertility traits, sourced from standard reproduction management data bases, are analysed for Holstein cows using bivariate linear-linear and linear-threshold animal models. Insemination events (n = 69 181) from 26 645 lactations of 9 046 Holstein cows from 14 herds, calving down during the period from 1991 to 2007, were available. The outcome of each AI event was known. Insemination records were linked to the calving date of each cow, lactation number as well as dam and sire identification. Fertility traits indicating the ability of cows to show heat early in the breeding period, and to become pregnant, were derived. Data were analysed using bivariate linear-linear and linear-threshold animal models with fixed effects being herd (14 levels), year (17 levels), season (4 levels) and lactation number (6 levels). The model included the random effects of animal and animal permanent environment (PE). Heritability estimates ranged from 0.04±0.01 to 0.10±0.02 for FS80d, from 0.07±0.01 to 0.08±0.02 for PD100d and from 0.06±0.04 to 0.08±0.02 for PD200d depending on the two-trait combination. Although heritability estimates of most fertility traits were below 0.10, they were in close agreement with results published by other researchers using linear models. Genetic correlations between different fertility parameters analyzed in this study indicated that it is unlikely that a single characteristic would serve well for selection purposes; instead, combining different traits could be used in selection programmes to improve fertility. Further research in constructing an optimal fertility index is warranted.

In the third part of this study, genetic parameters for South African Holstein cows for fertility and production traits were estimated from 2415 lactation records. Two-trait analysis of fertility and milk yield was investigated as a method to estimate fertility breeding values when culling, or selection based on milk yield in early lactation, determines presence or absence of fertility observations in later lactations. Fertility traits were days from calving to first service (CFS), days from calving to conception (DO), percentage cows inseminated within 80d post-partum (FS80d), number of service per conception (SPC), and the binary traits percentage of cows pregnant within 100d and 200d post-partum (PD100d, Pd200d). Milk production traits were 300 day milk, fat and protein yield. For fertility traits, range of estimates of heritability (h^2) was 0.006 to 0.08 for linear traits and 0.05 to 0.12 for binary traits. The range for permanent environmental variance (c^2) was 0.016 to 0.032. In this study genetic correlations of fertility with milk production traits were unfavourable ranging between −0.93 to 0.76.

Opsomming

Die beraming van genetiese parameters vir vrugbaarheidseienskappe en die invloed van melkproduksie op die reproduksie prestasie by Suid-Afrikaanse Holsteinkoeie

Kandidaat	:	**J. P. Potgieter**
Studieleier	:	**Professor K. Dzama**
Departement	:	**Veekundige Wetenskappe**
Fakulteit	:	**Landbou en Bosbou Wetenskappe**
Graad	:	**MSc (Agric)**

Winsgewende melkproduksie en genetiese verbetering in melkkuddes hang grootliks af van vrugbare koeie wat op ‘n jaarlikse basis kalf. Verskeie studies toon dat die reproduksievermoë van Holsteinkoeie oor die afgelope 30 jaar afgeneem het. Melkboere gebruik tussenkalfperiode (TKP) en aantal inseminasies per konsepsie (KIPK) as aanduidings van die reproduksievermoë van melkkoeie. Dit is egter moeilik om hierdie eienskappe as vrugbaarheidseienskappe vir melkkoeie te gebruik omdat TKP afhanklik is van opeenvolgende kalfdatums terwyl KIPK baie sterk gekoppel is aan die inseminasievermoë van die insemineerders. In die eerste gedeelte van die studie word alternatiewe vrugbaarheidseienskappe, wat afgelei is van inseminasie- en kalfdatums en die uitslag van dragtigheidsondersoeke, beskryf. Die invloed van ‘n aantal nie-genetiese faktore op dié eienskappe word ook bespreek. Gemiddeldes±standaard afwykings vir die periode vanaf kalwing tot eerste inseminasie (CFS), die periode van kalwing tot konsepsie (DO) was 77±30 en 134±74 dae onderskeidelik, terwyl die aantal inseminasies per konsepsie (SPC) 2.55±1.79 was. Die persentasie eerste inseminasies wat binne 80 dae na kalwing (FS80d), en die persentasie koeie wat dragtig bevestig is binne 100 (PD100d) en 200 dae na kalwing (PD200d) was 0.64±0.48, 0.36±0.48 en 0.71±0.45, onderskeidelik. Hoewel vrugbaarheidseienskappe betekenisvol beïnvloed is deur laktasienommer, jaar en seisoen van kalwing, het kuddes (bestuurders) die grootste effek op eienskappe gehad.

Vrugbaarheid is ‘n ingewikkelde eienskap en die uitdaging is om eienskappe te vind wat dit die beste beskryf. Genetiese parameters vir eienskappe wat oorweeg word sal ‘n aanduiding gee van die seleksieresponse in melkkuddes. In die tweede gedeelte van die studie is genetiese parameters van vrugbaarheidseienskappe en korrelasies tussen dié eienskappe beraam. Eienskappe is bekom vanaf reproduksiebestuursprogramme wat in melkkuddes gebruik word. Al die inseminasierekords (n = 69 181) van 26 645 laktasies van 9 046 Holsteinkoeie van 14 melkkuddes wat tussen 1991 en 2007

gekalf het, was beskikbaar. Die uitslag van elke inseminasie was bekend. Inseminasierekords is met die kalfdatum, laktasienommer, identifkasienommers van die moeder en vader van elke koei, gekoppel. Vrugbaarheidseienskappe wat die vermoë van koeie aandui om vroeg na kalwing op hitte te kom en beset te raak, is verkry. Die data is ontleed deur gebruik te maak van twee-eienskap liniêre-liniêr- en liniêr-drempel-diere modelle met vaste effekte kudde (14 vlakke), jaar (17 vlakke), siesoen (4 vlakke) en laktasienommer (6 vlakke). Die modelle het die ewekansige effekte van dier- en dier-permananente omgewingseffkte (PE) ingesluit. Genetiese, diere PE en residuele korrelasies is vervolgens beraam. Oorerflikhede varieer vanaf 0.04±0.01 tot 0.10±0.02 vir FS80d, vanaf 0.07±0.01 tot 0.08±0.02 vir PD100d en vanaf 0.06±0.04 tot 0.08±0.02 vir PD200d, afhangende van die twee-eienskap kombinasie. Ten spyte daarvan dat die oorerflikhede van die meeste vrugbaarseienskappe laer as 0.10 is, is die resultate in ooreenstemming met ander navorsers wat liniëre modelle gebruik het. Genetiese korrelasies tussen verskillende vrugbaarheidseienskappe toon dat daar nie enkel beste eienskap is wat vir seleksiedoeleindes gebruik kan word nie. Dit sou waarskynlik beter wees om verskillende eienskappe te kombineer om die vrugbaarheid in melkkoeie te verbeter. Verdere navorsing is nodig om ‘n optimale vrugbaarheidseienskap te ontwikkel.

Dit is belangrik dat die verband tussen reproduksie en melkproduksie vir melkkoeie bepaal word. In die derde gedeelte van die studie is genetiese parameters vir vrugbaarheid- en melkproduksie-eienskappe vir Suid Afrikaanse Holsteinkoeie beraam. ‘n Totaal van 2415 laktasierekords was beskikbaar. Vrugbaarheid en melkproduksie is volgens ‘n twee-eienskap analise ontleed as ‘n metode om teelwaardes vir vrugbaarheid te bepaal in gevalle waar die uitskot of seleksie gebaseer op melkproduksie in vroeglaktasie die teenwoordigheid of afwesigheid van vrugbaarheidseienskappe in latere laktasies bepaal. Vrugbaarheidseienskappe was die periode (aantal dae) tussen kalfdatum en eerste inseminasie (CFS), die aantal dae van kalf tot konsepsie (DO), die persentasie koeie wat by 80 dae na kalf vir die eerste keer geïnsemineer was (FS80d), die aantal inseminasies per konsepsie (SPC), en binêre eienskappe van die persentasie koeie wat by 100 dae en 200 dae na kalf beset was (PD100d en PD200d). Melkproduksie-eienskappe was 300-dae melk., vet- en proteïnproduksie. Vir vrugbaarheidseienskappe het die oorerflikheidswaardes (h^2) vanaf 0.006 tot 0.08 vir liniêre eienskappe gevarieer en tussen 0.05 tot 0.12 vir binêre eienskappe. Die permanente omgewingsvariansie (c^2) het tussen 0.016 tot 0.032 gevarieer. In hierdie studie was die genetiese korrelasies tussen vrugbaarheidseienskappe en melkproduksie-eienskappe ongunstig en het dit tussen −0.93 tot 0.76 gevarieer.

DEDICATION

This thesis is dedicated to my son Phillip, for his unconditional love, understanding and friendship. It is a privilege to be your father and having you in my life is the most important part of my existence.

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation and gratitude to the following people and institutions:

Professor K Dzama, in facilitating this study and being the study leader, for his support and guidance.

The whole research team at Elsenburg for their technical support and guidance.

Dr Oliver Zhisiri, for his friendship, guidance and motivation.

Mr. Sarel Cloete, for making data available from various dairy farmers that make use of the DIMMSA management programme.

My mother, Susan Potgieter, for her unwavering support and love.

My brother, Leon, for his support during difficult times.

My family and friends for encouragement and support.

Our Heavenly Father for the opportunity to finish this study.

TABLE OF CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

South African dairy farmers must continually strive to increase the productivity of their dairy herds because the industry's terms of trade (ratio of prices received to prices paid) are falling. The potential for dairy farmers to secure higher prices for their output to compensate for the increasing cost of production and downward pressure on product prices is very limited. Moreover, farming systems also need to be sustainable in terms of the environment and animal welfare. Hence, there is considerable interest in finding new ways of reducing costs and increasing efficiency at the farm level. Furthermore, the breeding goal of most dairy farmers is to increase the profitability of their milk production system. Most producers and breeders would add that this should be achieved without detriment to animal health, welfare and the environment. While there may be broad agreement on this aim, there is far less agreement on what the main components of profitability are, and how to improve these components most efficiently.

Until recently, milk production, including fat and protein yield, has been the main objective for selection in the dairy industries of most countries (Miglior, *et al*., 2005). Although milk production is clearly a major component of profitability, the emphasis it has received is also due to the ease of measurement compared to some other components of profitability. However, continued selection for higher milk production has been questioned on a number of accounts as it has been widely associated with deleterious effects on health, fertility and welfare of cows (Pryce & Veerkamp, 2001). Optimal financial performance generally comes from a high milk yield while maintaining a 365-day calving interval and an involuntary culling rate of less than 10%. Annual total culling rates should be kept at close to 18% to maximise the benefit of age and genetic improvement (Esslemont & Peeler, 1993; Ball & Peters, 2004). The effect of longer calving intervals, especially in seasonal calving systems, are manifested by lower annual milk yield, fewer calves sold per year, increased costs through a longer dry period and reduced profit associated with a move from a more profitable month of calving to one less profitable. Other increased costs associated with increased calving interval are more inseminations per conception and extra veterinary treatments.

Reduced reproductive performance has a significant negative effect on the profitability of a dairy herd (Britt, 1985; Dijkhuizen *et al*., 1985). Globally, there is a heightened concern about the declining trends in fertility and reproductive performance in dairy herds. Reasons for this trend have been partly attributed to the effect of Holsteinization or the use of North American genetics, and partly to the intense and prolonged selection for production traits, with the exclusion of functional traits like fertility, fitness and health-related traits. Declining fertility seems to be caused by a combination of various physiological and management factors, which start at calving, and which all have an additive effect on reproductive efficiency. Fertility traits, however, have a high environmental component, which implies that genetic improvement through selection is likely to be a slow process. Also, there is no consensus among authors regarding which trait(s) adequately defines a multi-dimensional character like fertility. Evidence of this is the inclusion of different fertility measures in national indeces by various countries. In South Africa inter calving period is currently being used as an indicator of fertility for Holsteins.

The rapid progress in genetics and management in the dairy industry throughout the world has created a new era in which a smaller number of cows have to meet the growing demand for dairy products. To meet the current demands, individual cows produce milk at a higher level and are found on farms with larger average herd sizes. Milk production of individual cows depends on their ability to become pregnant because the lactation cycle is initiated and renewed at calving (with the exception of induced lactation). In an effort to gain the greatest efficiency and lifetime productivity, dairy cattle are inseminated to establish pregnancy while they are lactating. Gestation and lactation therefore overlap until the dry period before the next lactation. Although the relative contribution of individual factors leading to infertility can be debated, the cumulative effect of these factors results in infertile cows which erodes the efficiency and profitability of the industry.

Fertility is either poorly, or not at all, accounted for in most dairy cattle breeding programs. There are several reasons for this, such as a difficulty in defining an appropriate trait which covers all aspects of fertility, problems in establishing an efficient recording system and uncertainties in modeling and evaluating data properly. In general, this reflects the fact that the whole process of reproduction is rather complex with numerous factors which have to act together to achieve a well-developed zygote and a finally healthy offspring. Moreover, fertility is influenced by both genes and the environment. However, although these two components act in unity, they synergistically mask the contribution of the other, thus confounding selection strategies for fertility and, ultimately, affecting reproduction performance (Pryce *et al*., 2004, Beever *et al*., 2006, Veerkamp *et al.,* 2007)

Fertility traits can be assessed according to three categories. The first would be to evaluate physiological characters like semen quality of bulls or hormone levels of luteinizing hormone (LH), follicle stimulating hormone (FSH) or progesterone in heifers and cows. However, these traits are not practical to measure on a population basis and are expensive to record. The second category for measuring fertility is related to various time periods within the lactation period starting from the previous calving date. The assumption would be that dairy farmers would like to get their cows pregnant as soon as possible after calving. Some of the traits used would be the interval from calving to first service (CFS), the interval from calving to conception (days open, DO), the interval between the first and last service (service or breeding period) and the interval between successive calvings (calving interval, CI). Calving interval is one of the most common traits used to determine reproductive performance of animals. Calving interval has some major drawbacks as an estimate of fertility (Hansen, 1979) because of the fact that two calving dates are required to determine CI while no CI records are available for heifers only calving once. Interval from calving to first insemination can be affected by the producer’s rational decision to breed the animal and can be recorded earlier than most interval traits. Days open (DO) can be influenced by semen quality and the technical ability of the inseminator and the success of heat detection. Interval traits are continuously distributed and are directly correlated to the economic and breeding goal of dairy producers.

A third category for measuring fertility can be described as success traits where reproductive performance are described using proportions of cows pregnant by specified time periods after their calving date. Various time intervals have been used, including 80 days (Uchida *et al.,* 2001), 100 days (Braun, 1986; Pursley *et al.,* 1997a), 115 days (Ferguson, 1996), 150 days (Henry, 1986; Gaines, 1989a; Markusfeld & Ezra, 1993; Mandebvu *et al.,* 2000; Raizman & Santos, 2002), 210 days (Ferguson, 1996) and 320 days (Raizman & Santos, 2002). Similarly, the proportion of the herd that recalved within 12 months of calving provides a single performance measure that describes the proportion of cows that conceive within approximately 83 days after calving and are retained to recalve (Esslemont, 1992). However, these traits are categorical (threshold traits) in nature and may require more complicated models for analysis. Examples of other fertility traits used include number of inseminations per conception and conception rate (whether cows became pregnant or not). The advantages of these traits are that they are available early after insemination (at pregnancy diagnosis) but are strongly related to management's efforts to get the heifers or cows pregnant.

1.1 Justification

Knowledge of reproductive performance of South African dairy herds is limited. National Milk Recording data only provides information on age at first calving (AFC) and CI. There is a need to describe current reproductive performance in South African dairy herds more accurately using appropriate measures, specifically traits that could be compared internationally. Fertility is increasingly being used in selection indexes, although the description of fertility and fertility traits seems to differ between countries. Milk recording data indicate that the milk yield of Holstein cows in South Africa has increased substantially over the last 20 years. Better feeding, management and genetic merit have resulted in higher milk yields of cows under most production systems. This has, however, resulted in a reduction in the reproductive performance of dairy cows as the higher milk yields were associated with an increased CI or, alternatively, the number of days open. In current literature there is an indication and a seemingly general consensus that the genetic relationship between the milk yield and reproductive performance of dairy cows is moderately unfavourable. This relationship also seems to be linked to a change in body condition in dairy cows especially during the early part of the lactation.

With the exception of two studies based on small data sets (Potgieter *et al.*, 2004) and a study of records from Holstein cows in three herds that calved from 1993 to 2004 (Muller *et al.*, 2006) no information is available in South Africa on genetic parameters for fertility traits of dairy cows. The reason for this is because insemination dates and confirmed pregnancies are not routinely recorded within the National Milk Recording Scheme. These insemination and calving records are only recorded within herds for management purposes.

The total daily milk yield in both commercial and small-scale dairy herds is affected by the number of cows in milk, stage of lactation and each cow's daily milk yield. A high daily milk yield is necessary for any operation to be economically sustainable in the long term. A negative effect on fertility would reduce farm income because more cows are in the later stage of the lactation when daily milk yield is lower. Fortunately the relationship between milk yield and reproductive performance is not unity; therefore the problem of poor reproductive performance could be overcome by improving reproductive management. In the long term a genetic selection index based on reproductive parameters and milk yield could arguably be used to improve both traits. The determination of genetic parameters for reproductive traits is a prerequisite for the construction of such a selection index.

1.2 Study objectives

The aims of the study are therefore the following:

1. to describe different fertility traits based on reproduction records such as calving dates, insemination dates and pregnancy diagnosis results;
2. to estimate genetic parameters for these fertility traits;
3. to estimate and compare breeding values for various fertility parameters from bivariate analysis of fertility traits and of fertility with milk production as a correlated trait; and
4. to make recommendations regarding the recording and analysis of appropriate information to determine the fertility of Holstein cows.

CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

Freeman (1984) predicted that the, "continued successful selection for production may depress reproduction to where selection on reproduction may be necessary" and proposed a challenge for reproductive physiologists to "develop new techniques to enhance reproductive performance so that selection will not be necessary". To a certain extent his challenge was answered in the sense that new reproductive management tools such as estrus synchronization were developed. However, genetic selection for improved reproductive performance of dairy cows is also needed since cow fertility has continued to decline (Lucy, 2001).

Over the last few decades, the dairy industry has changed dramatically. The rapid progress in genetics and management in the dairy industry throughout the world has created a new era in which a smaller number of dairy cows must meet the growing demand for dairy products. To meet the demands of the 21st century, individual cows produce more milk and are found on farms with larger herd sizes. The increase of milk production was the result of a combination of improved management and nutrition, intense genetic selection and biotechnology (Rajala-Schultz & Frazer, 2003). However, during the same period, little attention has been given to health and fertility traits (Pryce *et al*., 2004), which has led to serious deterioration of these traits due to their antagonistic relationships with milk yield (Andersen-Ranberg *et al*., 2003). The decline in fertility in modern dairy cows is a major concern (Lucy, 2001). Maintaining high reproductive efficiency in dairy cattle is a challenge and of the utmost importance, because it has the potential to have a significant effect on herd profitability (Britt, 1985).

Poor reproductive performance resulted in a substantial economic loss because of prolonged calving intervals, increased insemination and veterinary costs, higher culling rates, and increased replacement costs (Andersen-Ranberg *et al*., 2003). According to Freeman (1984) reproductive failures account for approximately 16% of all dairy cows culled in the United States. Thus, maintaining reasonable reproductive efficiency for dairy cows is becoming a challenging problem, which is of great importance for the profitability of the dairy industry (Hayes *et al*., 1992; Britt, 1985). Poor reproductive efficiency is a worldwide problem affecting the dairy industry. Some attempts were made to link poor reproductive efficiency to the increase of Holstein genes in dairy populations. The high conception rates of non-lactating Holstein heifers (70-80%) indicates that the problem is more complex and that milk yield could play a major role (Beam & Butler, 1999). This is particularly true if it is considered that milk production per cow increased by 218% and that these heifers are genetically primed to attain high milk yields. From this, it is evident that there is no clear consensus regarding the mechanism of the effect of yield on fertility.

Although the heritability of reproductive traits is accepted to be very low, there is evidence of sufficient variance to indicate that selection progress is feasible. Genetic progress for reproductive traits will be slow, but the dairy breeding industry needs to try to improve reproductive performance through genetic means. Because if its economic impact, dairy cattle fertility is receiving increasingly more attention by researchers throughout the entire industry. Reproductive costs are considered to be both direct and indirect expenses for producers. Direct expenses result from increases in breeding costs associated with increased inseminations per conception. Indirect costs result from decreased milk sales associated with longer calving intervals, an increase in the average days in milk of the herd and an inability to increase selection pressure because of greater involuntary culling (Averill *et al*., 2004).

2.2 Fertility and milk production

It may be assumed that genetic selection for improved female fertility is hampered by the dairy industry's strive for high milk production levels. There is overwhelming evidence that increasing genetic merit for yield, without considering genetic merit for fertility, reduces fertility (Pryce *et al*., 2001; Veerkamp *et al*,. 2003). The impact of this is such that, with single-trait selection for yield and an increase of genetic merit of approximately 1000 kg milk, calving interval is expected to increase between 5 and 10 days.

This expected genetic trend is also found in selection experiments (Pryce *et al*,. 2001). The observed phenotypic trend may in fact be higher or lower than this, depending on influences by management and nutrition. It is important to note that the association between milk production and fertility varies from herd to herd, both phenotypically (Windig *et al*., 2005) and genetically (Windig *et al*,. 2006). For example, the strength of negative associations between yield and fertility is equal to or lower in high production herds compared to low production herds (Castillo-Juarez *et al*., 2000; Kearney *et al*., 2004; Oltenacu & Algers, 2005). This finding supports the growing evidence that there is no fixed direct inverse association between phenotypic yield and fertility, and that reduced fertility due to selection for yield is not necessarily the consequence of the increase in yield per se (Weigel, 2006; Gutierrez *et al*., 2006).

Different mechanisms may underlie the clear negative genetic correlation between yield and fertility, e.g. pleiotropic gene effects, linkage or complex physiological associations (Veerkamp *et al*., 2003). Also, genetic selection for yield may change the energy partitioning in lactating dairy cows, causing a genetically induced negative energy balance and a lower body condition score (Veerkamp *et al*., 2003; Gutierrez *et al*., 2006). However, genetic associations between yield and fertility are such that conjoined improvement for milk yield and reproductive performance is feasible (Jamrozik *et al*., 2005; Andersen-Randberg *et al*., 2005; Royal *et al*., 2002) while maintaining 70–80% of the yearly increase in yield (Veerkamp *et al*., 2000). A practical example is given in Finish Ayrshire cattle (Pryce *et al*., 2001), where increasing the weight for fertility traits stopped the negative genetic trend in these traits that resulted from selection for yield.

Breeds selected for high production are more likely to be in extreme negative energy balance in early lactation and thus genetic correlations will be more unfavourable in such breeds, which might suggest that energy balance is inextricably linked with fertility. Lindhe & Philipsson (1998) reported that the genetic correlation between fertility and protein yield was more highly negative for Swedish Black and Whites with sires that were Holstein than for those with Swedish sires, suggesting a 'Holsteinization' effect on female fertility. But it could also be because selection for milk production has been more intense in the Holstein breed. Research by Royal *et al*. (2000c) found that the proportion of Holstein genes had no effect on commencement of luteal activity, although research in New Zealand has shown that fertility declines with an increasing proportion of international Holstein Friesian (HF) dairy cow genetics (Harris & Kolver, 2001).

Increased herd life or longevity is a highly desirable trait that affects overall profitability in the dairy industry. With increased longevity, the production of the herd increases. Firstly, a greater proportion of the culling decisions is based on production. Secondly, the number of older (third plus lactation) cows, which produce more milk than young (first and second lactation) cows, is increased. Longevity is determined by voluntary and involuntary culling decisions. Culling because of poor production is referred to as voluntary culling and culling for reasons other than poor production is referred to as involuntary culling. In the process of making culling decisions, producers will consider production, health, fertility, and other functional traits such as milking speed, milking temperament, and calving ease. Reducing the rate of involuntary culling allows a higher voluntary replacement rate, which can increase the net profit of a dairy farm. If the proportion of cows that conceive within a reasonable time is too low, voluntary culling rates have to be reduced to ensure that cow numbers do not decline. Therefore cows with low milk production are retained with consequent effects on herd profitability. Inadequate herd reproductive performance, manifested as prolonged calving intervals, increased involuntary culling, or both, can result in less milk and fewer calves per cow per year.

Milk yield is not the only factor that can affect reproductive efficiency. Lucy (2001) concluded that inbreeding has increased substantially in the Holstein population since 1980 and might play a crucial role in fertility. Additionally, Wolfenson *et al*. (2000) argued that reproductive performance in lactating dairy cows is extremely sensitive to heat stress in hotter regions. Oseni *et al*. (2004) reported similar results. An imbalance of nutrients, high genetic merit for production, or diets not matched to performance may all be causes contributing to poor reproductive performance. Physiological reasons for the antagonism have not been fully elucidated. To maintain or recover high fertility in modern dairy cows calls for a two-pronged approach involving both the inclusion of fertility in broader breeding goals as well as adjustment to management practices.

2.3 Fertility and parity

According to Hillers *et al*. (1984) older cows have a lower reproductive performance. Although cows in second lactation had reproductive performance equal to cows in the first lactation, cows in their third lactation or higher showed lower conception rates and longer intervals to first insemination than cows in earlier lactations (Hillers *et al*., 1984). Starbuck *et al*. (2004) found that retention of pregnancy varied with age of the cow, with younger cows tending to maintain more pregnancies (89.7%) than older cows (81.1%) but fewer fewer pregnancies than heifers (100%).

Generally, fertility is better in open heifers than in lactating cows. For example, Pryce *et al*. (2002) observed conception rates to first insemination of 64% and 71% in lines of open heifers of high and average genetic meri for production traits, while conception rates were 39% and 45% for lactating cows of high and average genetic merit in the same herd (Pryce *et al*., 1999). In both lactating and open heifers differences between the genetic lines for conception rate were significant ($P < 0.05$).

The interpretation of these results is that selection for milk production does lead to a decline in fertility (defined as conception rate) in both heifers and lactating cows. Although the semen quality between sires of high and average genetic merit for fertility could differ, it seems that the energy consumption of high and average merit heifers may not be different to high and average merit cows. Nevertheless, the genetic control of fertility may differ from heifers to cows. In this respect, genetic correlations between fertility in heifers and lactating cows ranged between 0.3 and 0.8 (Oltenacu *et al*., 1991; Weller & Ron, 1992; Roxstrom *et al*., 2001).

One explanation for overall conception rates being better in heifers and genetic correlations between heifer and lactating cow fertility being less than one, might be that the metabolic load is not as great in heifers as in lactating cows. Furthermore, as discussed by Royal *et al*. (2000a), the physiological status of cows and heifers are very different in that heifers reach puberty typically between 9 and 12 months of age, but are usually not inseminated until 15 months of age. The post-partum cow, on the other hand, has a shorter period in which to re-establish ovarian cyclicity before insemination.

Indeed, the hypothalamo-pituitary-ovarian axis in both heifers and post-partum cows must go through the occurrence of oestrus with ovulation, followed by normal luteal life span, to culminate in the establishment of ovarian function and pregnancy, if inseminated. However, following parturition, the post-partum cow must, in addition, undergo a series of additional recovery events, as reviewed by Malven (1984). These include recovery from pregnancy, including a reduction in high exposure to placental hormones, and escape from inhibition of gonadotrophins (caused by suckling).

Erb *et al*. (1981) hypothesized that another possible explanation for poor reproductive performance in older cows may be the more frequent occurrence of reproductive diseases with advancing age. Age was the most discriminating variable for retained placenta as well as the third most important discriminator between cystic follicles cases. Age is also associated with metritis. According to Gröhn *et al*. (1990) the occurance of dystocia, retained placenta and cystic ovary occur as a complex: dystocia is a risk for retained placenta, metritis and cystic ovary; retained placenta is a risk factor for metritis and metritis is a risk factor for cystic ovary.

In a study conducted by Fourichon *et al*. (1999) on the effects of disease on reproduction, it was found that metritis was associated with 7 more days to first insemination, 20% lower conception rate at first service and 19 more days to conception. The occurrence of cystic ovaries were associated with 6 to 11 more days to first service and with 20 to 30 more days to conception (Fourichon *et al*., 1999).

2.4 Fertility and the environment

When analysing fertility, non-genetic effects must be considred to produce unbiased estimates in genetic evaluations. Many environmental factors have been suggested to influence conception in dairy cows i.e herd, year, season of calving, month of insemination, level of production, age of the cow, the number of days post-partum when inseminated, service sire and the presence of disease such as mastitis. Most genetic models for fertility include herd, year and season effects (Thaller, 1998). Eicker *et al*. (1996) showed that conception rate varied with parity and season. According to Jansen (1985) fertility could vary with herd-year-season, parity and inseminator. In a study conducted by Miller *et al*. (2001) nonreturn rate was 7% higher in first parity than for sixth parity and later.

2.5 Fertility and genetics

Early theoretical analysis of quantitative genetic variation suggested that traits directly associated with fitness, such as fertility, should have low heritabilities and positive correlations among traits. Roff & Mousseau (1987) investigated the distribution of heritabilites for three categories of traits in *Drosophila,* i.e., fertility, behaviour and morphology. According to the literature, few morphological traits had heritabilities lower than 0.10 while heritability for most of the other traits ranged from 0.10 to 0.60 with a tendency of the standard errors to increase with the estimate. Heritabilites for behavioural and fertility traits fall within the 0.0 to 0.30 range. Heritabilty estimates for behavioural traits tended to be clustered within the region of 0.0 to 0.10 while the heritability estimates of fertility traits were evenly distributed.

According to the latter study, behavioural and physiological traits had heritabilities more like those of fertility traits than those of morphological traits (Roff & Mousseau, 1987). According to Roff & Mouseau (1987) physiological and behavioural traits are subject to constraints similar to those thought to influence fitness traits. This supported the suggestion made by Falconer (1989) that physiological traits generally have heritabilities intermediate between fertility and morphological traits.

2.6 Defining Fertility

Fertility is a composite and very complex trait, and it is difficult to define, to record and to evaluate all the factors that influence fertility. Darwash *et al*. (1997) defined fertility in dairy cows as follows: “the ability of animals to conceive and maintain pregnancy when served at the appropriate time in relation to ovulation”. Failure to establish a successful pregnancy could arise from failure to show or detect oestrus, failure to ovulate, inappropriate patterns of ovarian cyclicity, embryo or foetal loss (Royal *et al*., 2000b). Conception and maintenance of pregnancy in dairy cattle involves a synchrony between management effects and physiological processes (Darwash *et al*., 1999). Management issues include heat detection and timing of insemination. Physiologically, the fundamental prerequisite is the production of an ovum capable of being fertilised and a uterus capable of supporting pregnancy

(Darwash *et al*., 1999). Follicle development is controlled primarily by a feedback system involving gonadotrophin releasing hormone (GnRH), follicle stimulating hormone (FSH), luteinising hormone (LH), oestrogens, androgens and progestins and proteins (i.e. inhibin-related proteins secreted from the ovaries; Webb *et al*., 1994). Through the control of these, follicles grow in distinct waves that last 7 to 10 days. There are between two and four waves in an oestrous cycle of 21 days. Each wave involves the recruitment of a cohort of 5 to 7 primordial follicles of which one will become larger while the others will regress.

Determining how the selection process results in the selection of a single follicle from a cohort, as the others undergo atresia, is an area of intense research. Ireland *et al*. (2000) cited 19 studies that put forward both hypotheses and models on this subject. Dominance enables a single follicle to prevent the growth of other follicles or to grow in a hormonal milieu that is unsuitable for other follicles. Loss of dominance results in atresia of the dominant follicle, thus initiating growth of a new follicular wave. However, if the later growth of the dominant follicle coincides with luteolysis, it undergoes rapid maturation and ovulates. If fertilisation occurs successfully, the cow embryo remains free-living in the reproductive tract until implantation on about day 19 of pregnancy (Wathes & Wooding, 1980).

The problem with trait definition in genetic evaluations for fertility traits has been raised by several authors (Thaller, 1997; VanRaden & Tooker, 2003). Generally, fertility can be categorized into two classes as: (a) measures of success such as non-return rate, conception rate and number of inseminations to conception and (b) interval measures such as days open (DO), calving interval (CI), days to first service (DFS), breeding period, etc. Success measures are usually categorical, discontinuous characters, available early in lactation and requires sophisticated analyses, whereas the interval traits are continuous with substantial skewedness (Hoeschele, 1991; VanRaden & Tooker, 2003). In addition, interval traits have higher heritability than the success measures, but are highly dependent upon management (Norman *et al*., 2002).

2.7 Interval traits

Interval or continuous traits are most commonly used for fertility evaluation, in part because of their simplicity and availability at a large scale. Further, their analysis can be accommodated easily using existing standard tools, particularly mixed linear model methodology. Most interval traits, such as days to first service (DFS), calving interval (CI), and days open (DO) are likely to be influenced by management decisions regarding the potential yield or season of calving of individual cows (Stott *et al*., 1999; Butler & Smith, 1989; Darwash *et al*., 1997).

Given the non-uniformity and the effects of management decisions, interval traits (e.g. calving interval, days to first insemination, days open) tend to have low heritabilities (0.003 to 0.12); however, most estimates were around 0.04, which makes the identification of more fertile genotypes difficult and has consequently negated selection for fertility (Darwash *et al*. 1997).

2.7.1 Days from calving to first service (CFS)

Days from calving to first service tends to be inversely related to estrus detection in the early post-partum period (Bailie, 1982) and is the number of days from parturition to the first insemination of a given lactation. It is also influenced by the voluntary waiting period (VWP). The following table from a study by Bailie (1982) demonstrates the effect improving estrus detection efficiency has on days to first service.

Table 1 : The relationship between Days to First Service and Estrus Detection

	Mean interval to first service (days)*	Estrus detection efficiency (%)
** Volantary Waiting Period (VWP)	36	50
	31	60
	27	70
	24	80

* Assumed all cows were cycling normally and a conception rate of 60%.

** Assumed Volantary Waiting Period (VWP) of 50 days.

As can been seen from Table 1, days to first service is not within the optimal range (~75 days) (Pursley *et al*., 1997) to achieve a 13 month calving interval (Nebel & Jobst, 1998) until estrus detection efficiency reaches 80% (Bailie, 1982; Barnes, 2001). Lameness may affect days to first service due to lowered estrus detection efficiency in affected cows.

Days from calving to first service is regarded as one of the most important practical measures of reproductive performance. Weller (1989) used a large data set from the Israeli Holstein population to estimate the genetic parameters of days to first service in the first and second parities. Heritability of days to first service was 0.048 and 0.031 for first and second parity, respectively. The genetic and environmental correlations between days to first insemination in the first and second parities were 0.732 and 0.061, respectively. The genetic correlation between days to first insemination and production traits ranged between 0.2 and 0.3. However, these results have to be interpreted with caution because of the non-random selection applied to the data (only cows with records in both parities were considered).

2.7.2 First service to conception (FSTC)

The interval from first service to conception (FSTC), is derived from the interval from calving to first insemination, calving interval and an assumed gestation length of 280 days. FSTC reflects the ability of the cow to come into oestrus after calving and the ability to conceive successfully.

For the interval from first insemination to conception, high producing cows tend to have more opportunities for re-insemination in the case of failure of conception. FSTC is influenced by management decisions. The management bias on FSTC can be accounted for if information on culled cows could somehow be included in the analysis.

In a study done by Hoekstra *et al.* (1994), it was found that that the genetic standard deviation for FSTC was 6.4 days and the phenotypic mean was 22 days with a standard deviation of 39 days. The heritability for FSTC in the same study was 0.02. Jamrozik *et al.* (2004) reported a phenotypic mean of 16.3 (31.4) days for first lactation cows and 32.5 (44.4) days in later parities for FSTC.

2.7.3 Calving interval (CI)

A calving interval is the period of time between successive parturitions (usually reported in months on the herd level). Calving interval is most directly affected by three reproductive outcomes: estrus detection, days to first service, and voluntary waiting period (VWP), with estrus detection being the most important (Heuwieser *et al*., 1997; Nebel & Jobst, 1998). As calving interval increases, days in milk increases and lifetime milk yield decreases (Nebel & Jobst, 1998).

It was argued that economic losses due to poor fertility are the result of prolonged calving interval, increased insemination cost, reduced returns from calves born and forced replacement in the event of culling (Esselmont & Peeler, 1993). Using calving interval as a measure of fertility presents a problem because only animals that survive to the next lactation have a record for calving interval. Therefore, evaluations based on this trait alone could be biased as a result of culling of lowly fertile cows. To deal with the culling problem, Roxstrom & Strandberg (2002) and Olori *et al*. (2002) both recommended that calving interval should be treated as a censored trait and analyzed jointly with survival scores to consider the non-random scoring of calving interval.

Mayne *et al*. (2002) reported that herds with high heat detection rates had significantly shorter calving intervals and significantly lower 305-day protein yields, less body condition loss after calving, and significantly smaller negative energy balances. They concluded that calving interval shorter than 380 days is achievable by minimizing negative energy balance in early lactation, good heat detection, and early insemination of cows after calving.

Using Holstein data from New Zealand, the heritability for calving interval was estimated at 0.017 (Grosshans *et al*., 1996). This estimate is relatively low compared with other estimates. However, it is still within the range of reported estimates for the trait. The genetic correlations with milk production traits ranged from 0.026 to 0.22. Although lower than reported estimates, it still reflects the antagonistic relationship between reproductive performance and production traits. In a study conducted by Olori *et al*. (2002) single and multiple-trait models were used to analyze calving interval, survival rate and milk yield. The estimated heritability for calving interval in the three-trait model was 0.04 and the genetic correlation with milk yield was 0.4. The distribution of calving interval proofs from the single- and multiple-trait models were relatively similar. However, a left shift on the distribution of calving interval proofs suggests that analyzing calving interval alone, or along with survival rate without correcting for milk yield, may result in overestimation of breeding values for calving interval. Furthermore, the phenotypic trend indicated a steady increase in calving interval at the rate of 0.14 days per year from 1984 to 1995.

An extended calving interval is generally believed to reduce profit because efficiency of milk production is reduced, fewer calves are born and the rate of genetic gain is the herd is impaired (Westwood, 2002; Weller & Follman, 1990; Dijkhuizen *et al*. 1985; Oltenacu *et al*., 1981). Arbel *et al*. (2001) suggested that different results available in the literature on this subject were due to the different criteria and time periods used, yield levels and the seasonality of production patterns. Arbel *et al*. (2001) recognized that mllk production level and lactation persistency were crucial factors in determining the appropriate calving interval.

2.7.4 Days open (DO)

Calving to conception interval (CCI), also referred to as “Days Open” in some record keeping schemes, is the period of time between parturition and conception and is nearly always inversely related to estrus detection. This reproductive parameter is influenced by the estrus detection rate, conception rate, VWP, and culling (Bailie, 1982). Calving to conception interval plus gestation length, in turn, results in the intercalving interval (Bailie, 1982; Barnes, 2001). Realistically, calving to conception interval should be no more than 113 days to achieve an optimal calving interval of 13 months (Nebel & Jobst, 1998; Barnes., 2001). Calving to conception interval can be adversely affected by lameness. One study found that lame cows had calving to conception intervals of 40 days longer than healthy cows (Hernandez, 2001).

As days open increase:

1) fewer calves are produced per year leading to lower calf sales and fewer replacement heifers available for selection,

2) breeding costs increase due to higher services per pregnancy,

3) milk sold per day decreases due to longer average days in milk (DIM) (>150 days),

4) and veterinary costs increase due to more repeat breeders (Barnes, 2001; Walker *et al*., 1996).

In fact, the post-partum VWP, estrus detection efficiency, conception rate, and culling are the determinants of days open within dairy herds (Heersche & Nobel, 1994). Days open are also reported to increase with reproductive pathology, systemic illness, and lameness (Eicker *et al*., 1996).

The use of the interval traits, such as days open, focuses on the critical time period between calving and conception. Since there is generally little variation in the time from conception to parturition, management decisions emphasising to improve the time between calving down events, must be placed on the calving to conception interval. This time period can be divided into three major areas of emphasis:

- The time period between when the cow calves and when she becomes eligible for insemination. This period is typically called the Voluntary Waiting Period or VWP as defined previously.

- The efficiency with which cows are detected in estrus and inseminated following the VWP. The crucial input here involves estrus detection efficiency. It should be recognized that failures in estrus detection efficiency can result from either the failure of cows to have a regular estrus cycle or from the failure of management to identify and service the estrus once it occurs.

- The likelihood that a service or insemination will result in pregnancy. This factor is typically referred to as "Conception Rate" but a number of indices have been devised to measure the propensity for cows to become pregnant on each occasion that they are inseminated.

According to Misztal & Rekaya (2004), an interval trait like DO is a composite trait, with each component having a different distribution. These components are largely affected by management factors, including reproductive protocols (estrous synchronization and timed AI), use of lactation promotants such as BST, intentional delay in re-breeding, seasonal effects, etc. All of these factors were shown to affect the distribution of DO. These authors presented evidence showing that the distributions for this trait depended on BST use, herd production levels, season of calving and estrus synchronization status. They recommended that all these components be properly partitioned and evaluated separately.

Oseni *et al*. (2004) studied DO using five different upper bounds (150, 200, 250, 300, 365 days), using a large data set including DO records from several States in the US. By relaxing the upper bound from 150 to 365 days, means for DO increased by 25 to 50%, depending on the State. Similarly, the residual and genetic variances for DO increased with the increase of the upper bound. The estimated heritability ranged from 0.03 to 0.06. Genetic correlations of DO with milk production traits appear to be antagonist with estimates ranging from close to zero (Weller, 1989; Raheja *et al*., 1989a; Raheja *et al*., 1989b) to relatively high at 0.53-0.68 (Dematawewa & Berger, 1998). In addition, Marti & Funk (1994) studied the effect of milk yield and parity on DO. The regression coefficient of DO on milk production indicated an increase of around one and half days in DO for each additional 100 kg in milk yield.

Heritability estimates for DO are relatively higher than other reproductive traits. Available estimates ranged from almost zero to 0.15 and even higher. However, the majority of estimates ranged between 0.03 and 0.05, which is pretty much in line with estimates for other reproductive traits. (Brotherstone *et al*. 2002; Raheja *et al*. 1989a; Dematawewa & Berger, 1998; Hoeschele 1991).

2.7.5 Voluntary waiting period (VWP)

The voluntary waiting period represents the first portion of the calving interval. The duration of this period is partly a management decision, varying from 40 to 70 days on average. Part of its duration is based on the physiological need for the reproductive tract of the cows to undergo a involution, as cows are basically not fertile directly after calving. This changes quickly in the weeks following calving as the uterus involutes and returns to normal size and normal estrus activities resume. Some studies indicate that longer calving intervals improve conception rates, possibly because of improvements of various uterine traits. However, when cows calve down without any complications, this recovery process requires no more than 40 days (Stevenson, 2001)

Any cow that has had some type of reprocutive or metabolic incident at calving needs more time to recover. They typically return to normal estrus about one heat cycle later than herdmates that calved without difficulties.

2.8 Binary traits

The recent theoretical and computational developments in the analysis of discrete and binary data have made the use of binary traits for reproductive performance evaluation possible. Although these traits were analyzed for a period of time as continuous responses using existing mixed linear methodology, in clear violation of their distributional assumptions, the threshold liability model is becoming the standard tool for discrete data analysis, especially after the papers by Best *et al*. (1995) and Sorensen *et al*. (1995). There are several binary traits used as measures of fertility. However, conception rate (CR) and non-return rate (NRR) after a fixed number of days (e.g. 70 or 90 days) and success or failure of an insemination were the most widely used binary traits found in the literature. All these traits are in some sense connected and tend to have lower heritability estimates, especially when analyzed with mixed linear models. Compared to interval traits, binary responses are usually measured early during the lactation which will reduce the impact of environmental and management effects and allow for early genetic evaluation (Thaller, 1998). Non-return rate has mostly been used as a measure of male fertility, and it depends on complete recording of all subsequent inseminations. Furthermore, a calving date is not required. Weigel & Rekaya (2000) used non-return rate at day 70 (NR70) and 90 (NR90) for the joint evaluation of male and female fertility. The cow being inseminated was considered as the animal to estimate additive genetic effects (female fertility), while the service sire (male fertility) was considered as a random environmental effect (representing a combination of genetic and permanent environmental effects). They used a linear and threshold model for estimating genetic parameters for NRR and confirmed pregnancy at 60 and 90 days post-partum in dairy herds in California and Minnesota.

Linear model variance component estimates were lower than threshold model estimates except for phenotypic variance in Minnesota herds. They argued that the inflated phenotypic variance in Minnesota herds could the result of small herd size in Minnesota compared to California herds and to the use of herd-season as contemporary group instead of herd-month. The correlations between NRR and confirmed pregnancy at day 60 (CP60) were high, ranging from 0.88 to 0.92 and lower between NRR and CP90 (0.66 to 0.84) indicating a potential error (misclassification) of pregnancy status. Further, the lowest NRR was observed in winter (November to February) and the highest in spring (May to June). Schnyder & Stricker (2002) used a bivariate linear animal model to estimate variance components for days to first service and non-return rate in three breeds (Holsteins, Red and Whites, and Brown Swiss). The estimated genetic and service sire variance components ranged from 0.007 to 0.011 and 0.0013 to 0.0023, respectively. Heritability estimates were below 0.04 for all three breeds with the lowest estimate of 0.03 being derived for the Red and White breed. The genetic and residual correlations between NRR and interval from calving to first insemination ranged from respectively 0.22 to 0.31 and –0.06 to 0.04. Andersen-Ranberg *et al*. (2002) reported a 3.7 and 2.8% increase in NR rate for heifers and first lactation cows, respectively during a twenty-year period (1979-2000).

The major problem with NRR as a measure of reproductive performance was highlighted by Mayne *et al*. (2002) who reported that the average conception rate to first service was 37.1%, or 16% less than the CR estimated from the 60 day NRR in the same herds. This difference illustrates the unreliability of accepting the 60 day NRR as proof of a successful mating. Taylor *et al*. (1985) used conception rate as a measure of fertility performance and found that both the additive (0.016) and service sire (0.005) variance components were low compared to those obtained using NRR. Further, their results suggest higher conception rate in fall months compared with winter months, and the largest difference, 6.1% was observed between October and January. Jansen (1986) used a linear model to estimate genetic parameters for non-retrun rate 56 days NR56 and conception rate for heifers and cows. Heritability estimates were relatively similar for NR56 and CR, although a few discrepancies were observed. NR56 heritability ranged from 0.1 to 0.023. Parity one had the highest heritability for NR56 and parity two had the highest heritability for CR. Hodel *et al*. (1995) analyzed non-return rate on heifers and cows using a bivariate model and reported higher service sire and additive variance components, as well as higher heritability estimates using cow data.

This study concluded that the maximum fertility appears to be achieved approximately 120 days after calving and that inseminating cows before 45 days after calving is not advisable, because the uterus requires a longer recovery period. Clay & McDaniel (2001) reported that cows bred within 50 days after calving are expected to have a 5.5% greater chance of being rebred within 70 days post-partum than cows bred between days 70 to 79 days post-partum. Similarly, cows bred at more than 139 days post-partum were expected to have 3.3% less chance of being rebred within 70 days than cows bred at 70 to 79 days post-partum.

2.9 Count Traits

The only count trait used, as a measurement of fertility, was the number of services (inseminations) to conception (NS). If inseminations are conducted at regular intervals, it reflects the ability of the cow to start cycling after calving and her potential of becoming pregnant. However, it is seldom the case that inseminations are carried out at regular intervals. Furthermore, censoring is a major problem when analyzing NS as too many cows have incomplete records. Additionally, NS is not a continuous trait and its analysis requires special methodology (poison models) and software. As a result, only a few studies have looked at this trait. Raheja *et al*. (1989a) reported that NS ranged from 1.54 to 1.55 for the first three lactations. Heritability estimates increased with lactation number from 0.03 to 0.06 for first and third lactation, respectively. In another study, Raheja *et al*. (1989b) used a mixed linear model to analyze NS as a measure of female fertility and NRR as a measure of male fertility. The estimated genetic and phenotypic correlations between these two traits was low at -0.09 and -0.012, respectively.

Dematawewa & Berger (1998) used a repeatability model for NS across lactations and reported estimates of 0.028 for heritability and of 0.083 for repeatability. Heritability estimates from across parity analyses ranged from 0.01 (second lactation) to 0.11. Foulley *et al*. (1987) were first in developing a poisson model for analysis of count data. Tempelman & Gianola (1996) used such a model for analysis of NS in Holstein heifers. They reported an estimated heritability of 0.026, which is similar to estimates of other discrete fertility traits.

2.10 Conclusion

Until recently, fertility traits were not seriously considered in most breeding programs for several reasons, including the lack of unified definitions for reproductive performance, the lack of an efficient recording system and the theoretical and computational complexity in modeling and analyzing such data. Pryce *et al*. (2004) stated that the limitation in using insemination data is, in part, because of the considerable variation in the recording quality.

Fertility is a complex trait that is becoming more and more important for genetic improvement programs in dairy cattle. Long-term single-trait selection for predominantly increased milk production had a negative impact on several secondary traits including fertility.

Most interval traits used as a measure of fertility are influenced by management decisions and production levels, which could potentially lead to non-ignorable bias. Some discrete or binary traits are less affected by management decisions and could potentially be instrumental in improving reproductive performance in dairy cattle genetically. However, the theoretical and computational complexities associated with their use and the non-availability of a national recording system of these traits could limit their extensive use.

Although the heritability of fertility traits are low, ranging from one to ten percent depending on the definition of the trait and the methodology used for analysis, there is consensus that sufficient genetic variability exists, and it can be exploited to improve reproductive performance genetically. Depending on the trait definition, different models and methodologies have been developed and implemented in this study to analyze reproductive performance.

CHAPTER 3

NON-GENETIC FACTORS AFFECTING FERTILITY TRAITS IN SOUTH AFRICAN HOLSTEIN COWS

3.1 ABSTRACT

Profitable milk production and genetic improvement in dairy herds depend largely on fertile cows capable of calving down on an annual basis. Several studies indicate declines in the reproductive performance of dairy cows over the past decades. Reproductive performance of cows is related to calving interval (CI) and services per conception (SPC). Using these traits as cow fertility indicators is problematic, as CI depends on subsequent calving dates, while SPC is strongly linked to inseminator proficiency. Non-genetic factors affecting alternative reproduction traits to CI in Holstein cows are discussed in this chapter. Means±sd for the interval traits calving to first insemination (CFS) and interval from calving to conception (DO) were respectively 77±30 and 134±74 days while the number of services per conception (SPC) amounted to 2.55±1.79. The percentage of first inseminations occurring within 80 days post-partum (FS80d) and the percentage of cows being confirmed pregnant within 100 (PD100d) and 200 days post-partum (PD200d) were 0.64±0.48, 0.36±0.48 and 0.71±0.45, respectively. While lactation number, calving year and month affected reproduction traits significantly, herds (managers) had the largest effect.

3.2 INTRODUCTION

Female fertility is an economically important trait in dairy cattle production. Genetic evaluation of fertility is difficult, mainly because of incomplete data recording in industry. According to Weigel *et al.* (2004) most reproductive traits are affected profoundly by differences in herd management practices and other environmental factors. However, research has indicated that significant additive genetic variation exists for certain measures of reproductive performance. Therefore, it could be possible to improve reproductive performance when included in breeding programs.

The availability of insemination data provides the opportunity to calculate intervals, count records and success traits as measures of dairy cow fertility. Such interval traits include the interval from calving date to first service date and first service date to conception date. These traits have become important in predicting reproductive performance in several studies (Averill *et al*., 2004; Jamrozik *et al*., 2005; Biffani *et al*., 2005). These studies and others have also confirmed that reproductive performance of cows can be broken up in several components. For genetic selection to be effective, it is essential to understand the biological behaviour of reproductive traits, especially the real genetic and environmental contributions to the phenotype for these traits and the magnitude of the response selection. Identification of superior animals and subsequent selection decisions should be based on genetic merit rather than on differences due to environmental effects (Safari *et al*., 2007).

Developing effective genetic evaluation and improvement programmes requires knowledge of the genetic parameters and environmental effects that need to be adjusted for in economically important traits. These parameters need to be estimated from relevant populations as parameters and fixed effects may vary among breeds and different populations (Safari *et al*., 2007). Environmental factors have a very large effect on fertility (Hayes *et al*., 1992). Herd management, year, season and parity were some of the factors that affected fertility in different studies.

Breeding and selection programmes in dairy herds in South Africa in the past have focused mainly on the improvement of milk yield and conformation traits. Although the reproductive performance of dairy cows affects a herd's profitability, local dairy farmers put little emphasis on the improvement of cow fertility. At best, non-pregnant cows are culled because of reproductive failure. This is also done only after a considerable effort was put into getting such cows pregnant. This typically includes a large number of services, hormone treatment sessions and using natural service by a home-bred bull. This usually results in a protracted service period.

Poor reproduction management could be reflected as poor fertility in cows. Selection for higher milk yields in dairy cows has led to a decline in the fertility of dairy cows because of unfavourable genetic correlations between milk production traits and fertility (Pryce *et al*., 2004). In South African Holsteins, calving interval (CI) increased from 386 days in 1986 to 412 days in 2004 (Makgahlela, 2008). Recently, Mostert *et al*. (2010) reported on genetic parameters for CI for the four major dairy breeds in South Africa. Although this is a first step towards the genetic evaluation of the fertility of South African dairy cows, Haile-Mariam & Goddard (2007) pointed out that while CI is used for the genetic evaluation of dairy cow fertility, cows that do not re-calve for any reason, including those cows culled for not becoming pregnant, for whatever reason, are not included in a genetic evaluation for this trait. This means that information on the perceived least fertile group of cows is excluded, possibly leading to inaccurate estimated breeding values for their sires.

Management level in dairy herds may influence fertility traits with traits being lower in poorly managed herds. Using AI dates and the results of pregnancy examinations, additional information regarding the reproductive performance of dairy cows is obtained. From such information, genetic parameters for some fertility traits have been estimated for small data sets, i.e. 2639 lactation records of 751 Jersey cows (Potgieter *et al*., 2004) and 3642 lactation records of 1375 Holstein cows (Muller *et al*., 2006). Heritability estimates for key fertility traits were within the range of estimates from overseas studies.

Recently, breeding values for a number of alternative reproduction traits have been published for Holstein cows (Mullereever *et al*., 2010) using a larger data set. In Canada, a national recording scheme for fertility traits has been implemented as part of a new milk recording scheme (Jamrozik *et al*., 2005). Insemination data have been accumulated since 1997 and a national genetic evaluation program for fertility traits of cows has been developed. Van Doormaal *et al*. (2004), reported preliminary results for four fertility traits, i.e. age at first service in heifers, non-return rate to 56d in heifers and cows and the interval from calving date to first insemination date for Canadian dairy breeds. Jamrozik *et al*. (2005) also considered fertility traits such as the number of days between calving and the first insemination date, the number of inseminations, and the number of days between first service to conception. Other traits included age at first service, first service non-return rate to 56 days, calving ease, calf size, stillbirth and gestation length.

Heritability estimates of fertility traits were low, ranging from 3% for non-return rate in heifers to 13% for age at first service. Jamrozik *et al*. (2005) concluded that female fertility is a complex set of traits affected by both genetic and environmental factors. Genetic correlations between these different fertility parameters indicated that there is not likely a single characteristic that would serve well for selection purposes. Different traits should be combined in a fertility index.

Fertility could be defined as the successful birth of a calf following a timely (short) conception followed by a normal gestation period. This chapter presents non-genetic factors affecting alternative reproduction traits to CI in Holstein cows.

3.3 MATERIAL AND METHODS

3.3.1 Data.

All artificial insemination (AI) records (n = 69 181) of cows calving down between 1991 and 2007 in 14 South African Holstein herds were used. A total of 24 646 lactation records of 9 046 individual cows was available. The outcome of each AI event was known. Pregnancy diagnosis was based on rectal palpation by a veterinarian, usually during a monthly farm visit. Cows experiencing calving problems or other problems such as retained placentas were treated by a veterinarian as required. Insemination records were linked to the calving date of each cow, lactation number, dam and sire identification numbers. By using this information, fertility traits that measure the ability of cows to show heat early in the breeding period and the probability of the success of insemination and confirmation of pregnancy were derived. These traits included the following: interval from calving date to first service date (CFS), the interval from calving date to conception date (DO), number of services per conception (SPC), whether cows were inseminated within 80 days post-partum (FS80d), whether cows were confirmed pregnant within 100 (PD100d) and 200 days post-partum (PD200d). Non-interval traits were recorded as binary threshold traits coded as 1 = no and 2 = yes. Reproduction records exceeding three standard deviations from the mean for each trait were deleted from the data set.

3.3.2 Statistical analyses.

To determine which fixed effects should be included in the model, an analysis was carried out using the General Linear Models (PROC GLM) procedure of GenStat Seventh Edition software (Lawes Agricultural Trust, 2007). The REML Linear Mixed Models (LMM) procedure was implemented for continous traits and the Generalized Linear Mixed Model (GLMM) procedure was used for binomial traits via a LOGIT link back transformation. Significant ($P<0.05$) fixed effects that were subsequently incorporated into the final model were herd (14 levels), year of calving (17 levels), season of calving (4 levels) and lactation number (6 levels). The GLMM models included herd as a random factor (De

Vries & Risco, 2005). Least square mean estimates and REML solutions for the significant fixed effects were also derived.

3.4 RESULTS AND DISCUSSION

3.4.1 Descriptive statistics.

Cows eventually became pregnant in most lactations (0.85±0.36). The number of services per conception (SPC±s.d.) was 2.55±1.79 indicating a less than average insemination efficiency of 0.39 (Table 3.1). Haile-Mariam *et al. (*2004) reported a substantially lower value of 1.85 for SPC. Although average values for some traits were acceptable, large variation was observed as indicated by high standard deviations. The coefficients of variation (%) for interval traits was 39% for CFS and 70% for SPC. The interval from CFS averaged 77±30 days with 64% of first services occurring within 80 days post-partum. The interval from calving to conception (DO) was high and variable at 134±74 days. Only in 36 and 71% of all lactations were cows confirmed pregnant within 100 and 200 days post-partum, respectively. Observed values for these traits are the result of a complex interaction among several elements such as the decision policy of the dairy farmer, physiology, nutrition, management, environmental factors and genetics. Therefore, a considerable spread of values is to be expected.

Table 3.1 Descriptive statistics for the raw data analyzed for fertility traits, i.e. interval from calving to first service (CFS), interval from calving to conception (DO), number of services per conception (SPC), whether cows were inseminated for the first time within 80 days post-partum (FS80d), whether cows were confirmed pregnant within 100 days post-partum (PD100d) and whether cows were confirmed pregnant within 200 days post-partum (PD200d) (CV = coefficient of variation)

Variables	CFS (days)	DO (days)	SPC	FS80d	PD100d	PD200d
Number of records	16 605	14 255	14 255	16 648	16 648	16 648
Mean	77.3	133.9	2.55	0.64	0.36	0.71
Standard deviation	29.9	74.3	1.79	0.48	0.48	0.45
CV (%)	38.7	55.5	70.2	75.2	133.7	64.0
Minimum	21	21	1	0	0	0
Maximum	250	435	8	1	1	1

The CFS interval was less than 100 days in 82% of cases. However, first AI success rate was less than 40% resulting in a long 1stAI-conc interval which in turn resulted in a high number of days open. Only 42% of DO intervals were concluded within 100 days post calving, while 18% dragged on for longer than 200 days after calving.

The effect of herd, year of calving, season of calving and lactation number on fertility traits is presented in Table 3.2. Herd had the largest effect on the variation within traits. This variation is probably related to management style and inseminator proficiency.

Table 3.2 Degrees of freedom and total sums of squares (or mean squares), depicting the effects of herd, year of calving, season of calving and lactation number on fertility traits in South African Holstein cows (CFS = interval from calving to first service; DO = interval from calving to conception, SPC = services per conception; FS80d = percentage of cows inseminated within 80 days post-partum, PD100d = percentage of cows confirmed pregnant with 100d post-partum, PD200d = percentage of animals confirmed pregnant within 200d post-partum)

	Fixed effects			
Traits	Herd	Calving year	Calving Season	Lactation number
Degrees of freedom	13	16	4	5
CFS	2598201**	118646**	25816**	75173**
Days open (DO)	1259070**	2273999**	21501[1]	331422**
Services per conception (SPC)	1473.72**	1059.98**	27.903[1]	34.05[1]
FS80d	487.64**	41.39**	6.09**	11.81**
PD100d	119.71**	25.44**	9.15**	14.68**
PD200d	196.92**	37.32**	7.54**	32.31**

**P<0.01; *P<0.05; [1]Not significant

3.4.1.1 Interval between calving date and first service date (CFS)

The interval between calving date and first service date as affected by herd is presented In Figure 3.1. CFS intervals indicate large differences between herds, i.e. minimum and maximum intervals were 57 and 100 days respectively. This finding emphasises the large effect of management style. The feeding management of herds varied from zero-grazing to pasture based farms with a corresponding large variation in production performance. No information was collected on each manager's management style to give some indication of the reason for the observed differences. According to Table 3.1 herd had the biggest contribution to the total variance for CFS. The largest difference in days from calving to first service was between herds 11 and 14, differing by 43 days (Figure 3.1). Such differences could could be associated with poor heat detection or cows not showing heat because of reproductive problems like metritis. Failure to detect signs of heat after calving would prolong the interval from calving to first service. Farmers often have different policies pertaining to voluntary waiting periods (VWP), A prolonged interval between calving and first service could also be associated with a low nutritional status of the cows, not allowing them to recuperate fast enough after calving. This could, however, result in extended calving intervals. Furthermore, because of poor overall AI efficiency, which is a human factor, the fertility of dairy cows could be perceived to be poor.

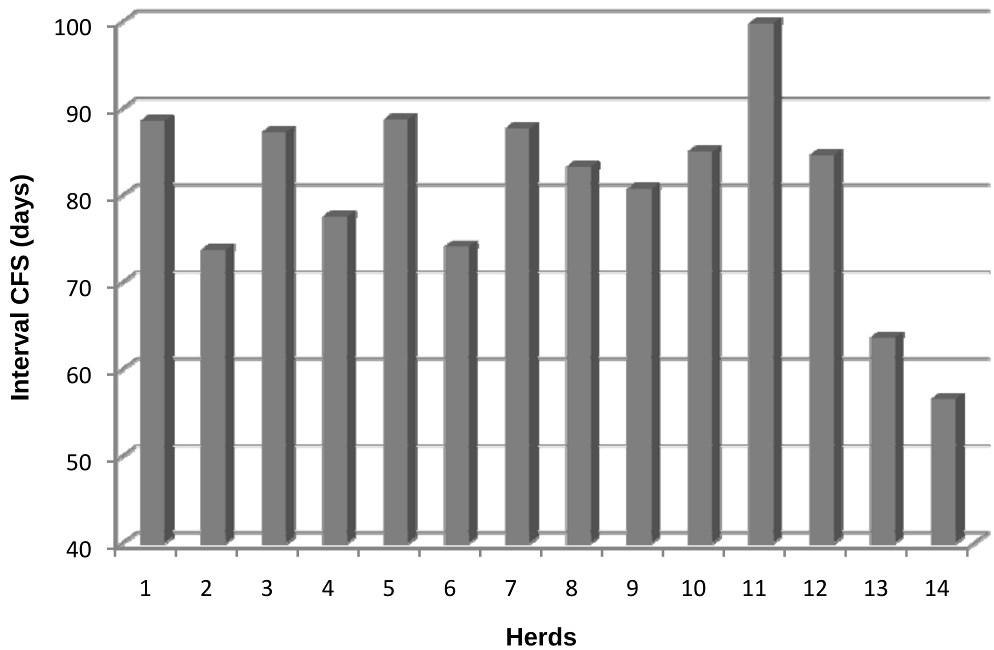

Figure 3.1 Collumn graph depicting means for the interval between calving and first service date for all cows in 14 Holstein herds

The change over time in interval between calving date and the first insemination date as affected by calving year is presented in Figure 3.2. Generally, it seems that the CFS interval increased over time from 1991 although the linear trend was small (0.24 days per year) and not-significant ($P>0.05$; R^2 = 0.11). The largest increase occurred from 1991 to 1994 when the annual increase was 3.5 days (R^2 = 0.75; $P<0.05$). From 1995, the CFS interval did not change over time, probably indicating the inability of herd managers to improve on this trait. De Vries & Risco (2005) also showed that the number of days from calving date to first service date for Holstein cows in Florida and Georgia increased from 84 in 1983 to 104 days in 2001.

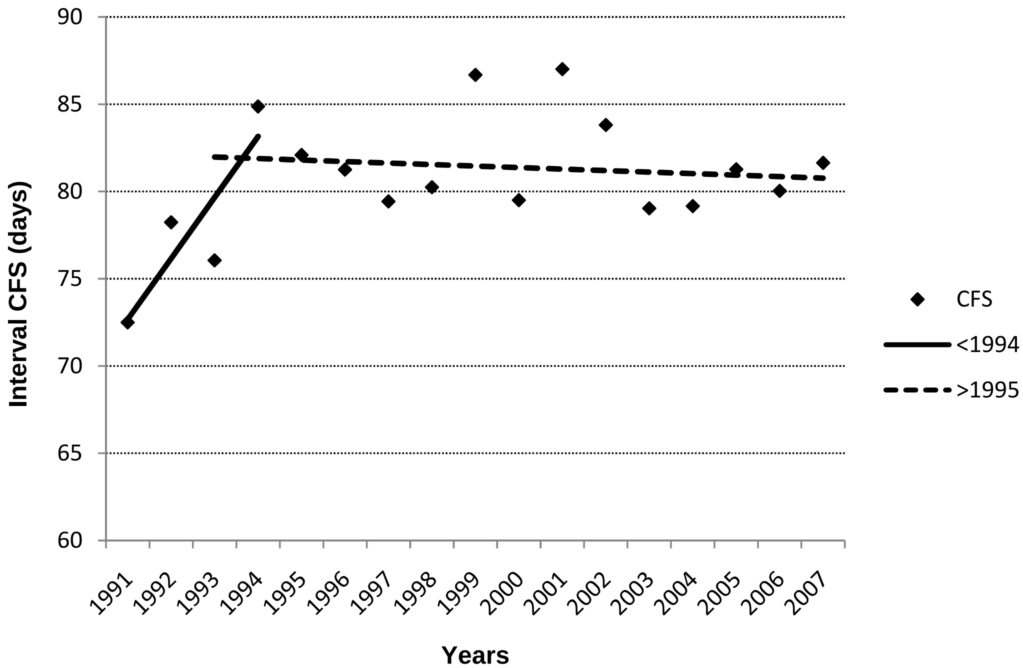

Figure 3.2 The interval between calving date and first service date for all Holstein cows as affected by calving year (<1994: y = 69.2+3.5x; R^2=0.75, >1995: y=82.2-0.09x; R^2=0.02)

The percentage of first inseminations being done within the first 80 days after calving is 64%, which indicates that a significant number of first inseminations occurs much later after calving. The reason for this could be ascribed to the management of cows immediately following calving i.e. cows having uterine infections or reproductive problems such as cystic ovaries not observed early by managers. Uterine infections could be caused by a number or factors such as calving environment (wet and dirty conditions), the birth weight of calves (sire selection), the presentation (position) of calves during the birth process and retained placentas because of nutritional imbalances. This could be addressed by examining cows on a daily basis during the first 10 days of the lactation period. Possible signs to look for include, retained placentas, an increase in body temperature (as reflected by rectal temperature), bloody and smelly vaginal discharges, dried vaginal discharges on the pin bones, erratic movements of the tail and sunken eye sockets because of dehydration.

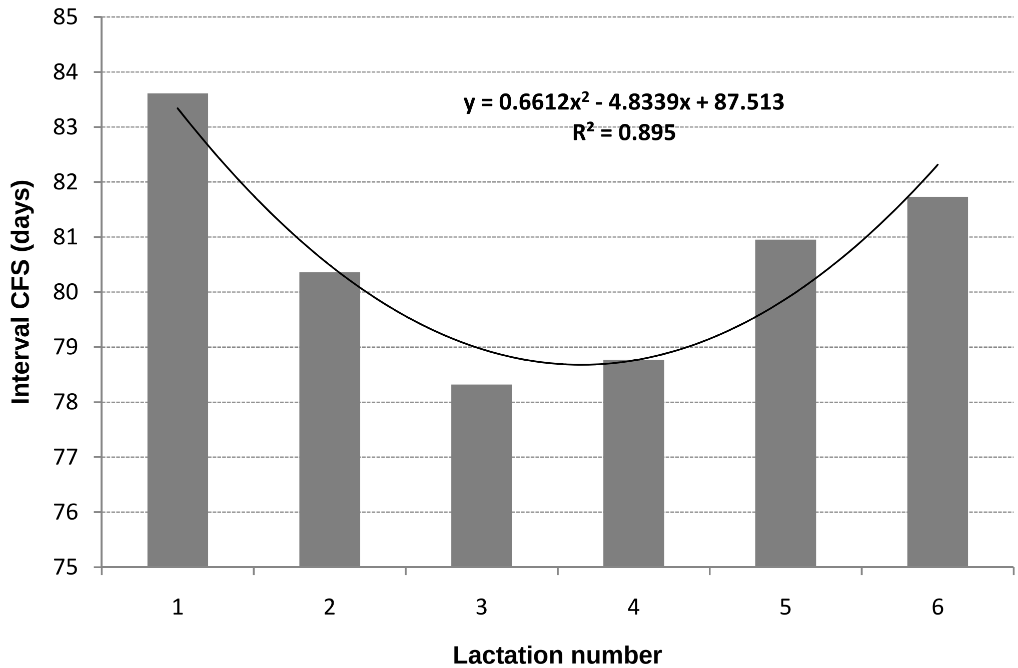

Figure 3.3 The change in the interval from calving to first service for all cows in 14 Holstein herds as affected by lactation number.

Parity affected the means for days from calving to first service significantly ($P<0.05$; Figure 3.3). The average days from calving to first service decreased from 84 to 78 days, from parity 1 to parity 3, after which the number of days between calving and first service increased to 82 days. The reason for this trend is not clear, however, physiological stress at first calving could affect young cows, partly explaining the observed longer CFS. The second explanation is the fact that after the first parity, animals continue to grow whereby the dietary energy intake is partitioned to meet the requirements for maintenance, continuation of growth, lactation and reproduction.

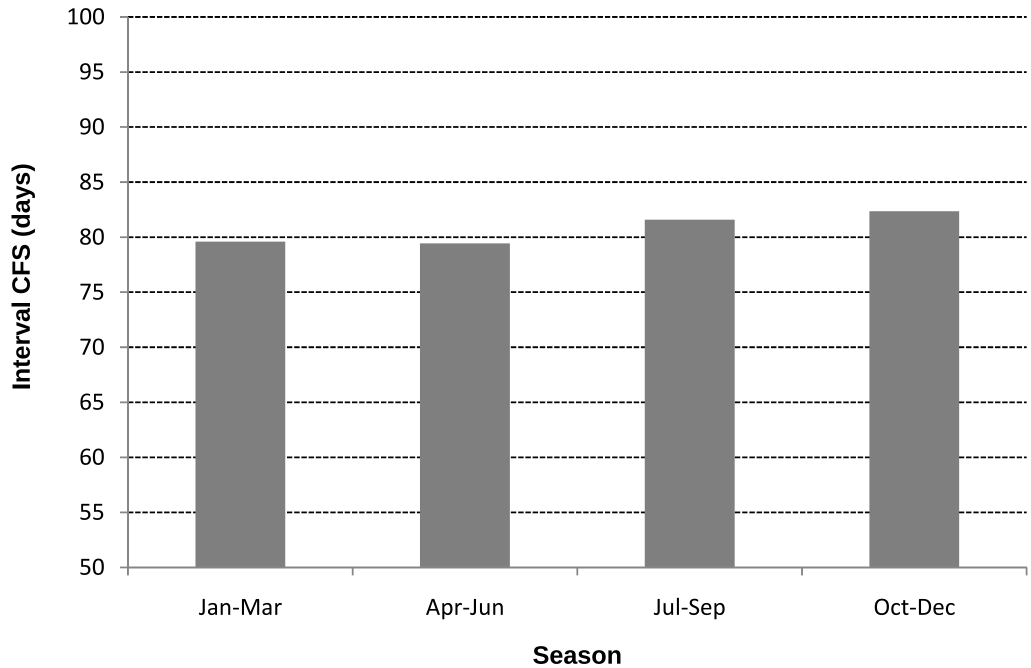

Figure 3.4 The change in the interval from calving to first service for all cows in 14 Holstein herds as affected by season of calving.

Season of calving affected the interval between calving and first service significantly (P<0.001; Figure 3.4), although the absolute difference in the number of days was small. Cows calving from January to June had the shortest interval from calving to first service (79.4±0.6) while cows calving from July to December had the longest intervals (82.4± 0.7). The reason for this could be ascribed to the rainfall pattern because most herds used in the study were in the summer rainfall area, which means that cows calving down in summer had to cope with wet conditions. This could cause more cows having metritis problems because of a dirty calving environment.

3.4.1.2 Interval between calving date and conception (DO)

One of the measures of fertility in dairy cattle is days open (DO) as determined from the interval (number of days) between calving date and conception date. Days open is a complex trait that can be affected by many factors, such as season of calving, management policies, herd size, parity, as well as AI technique. In this study, DO included the actual number of days from calving to conception for cows confirmed pregnant, plus estimated days to conception for non-pregnant cows. The overall mean number of days open in this study was 134±74 (Table 3.1) with a coefficient of variation of 56%. In Figure 3.5 the mean number of days from calving date to conception date is presented for 14 Holstein herds used in this study. According to Table 3.2 herd had the biggest contribution to the observed total sums of squares for DO. The largest difference in number of days open (P<0.001) was between herds 11 and 13, which differed on average 77.8±6.8 days between calving and conception.

The interval between calving date and conception date differed (P<0.01) between herds with minimum and and maximum number of days open (DO), being respectively 105 and 183 days. Differences between herds probably indicate management levels such as inseminator proficiency.

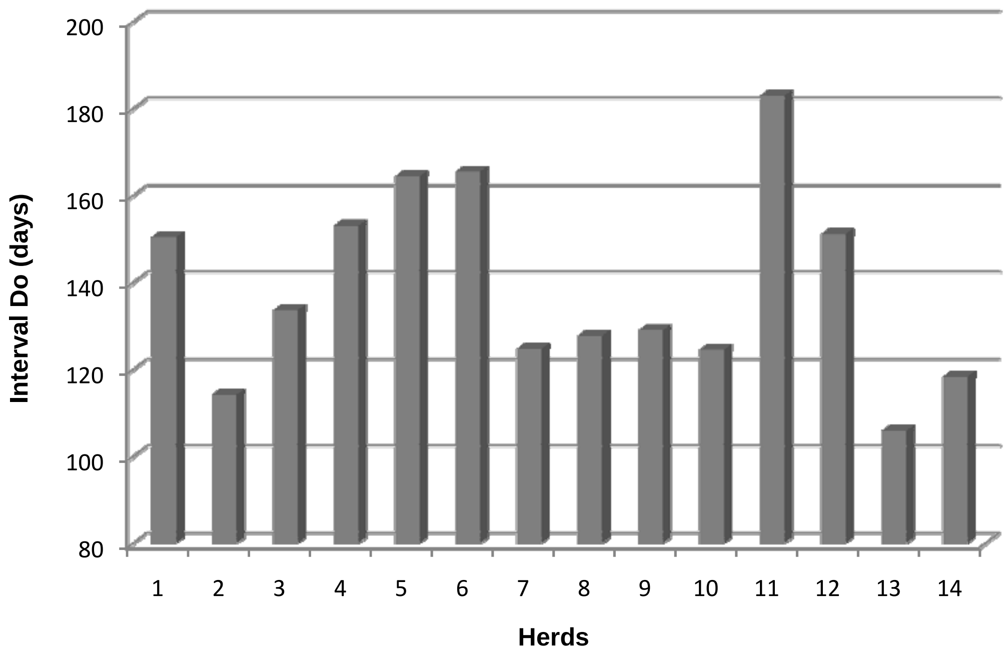

Figure 3.5. The mean number of days from calving date to conception date (DO) for 14 Holstein herds

The variation of DO from one herd to another could be attributed to differences in skills of heat detection, differences in voluntary waiting periods (VWP) and conscious management decisions.

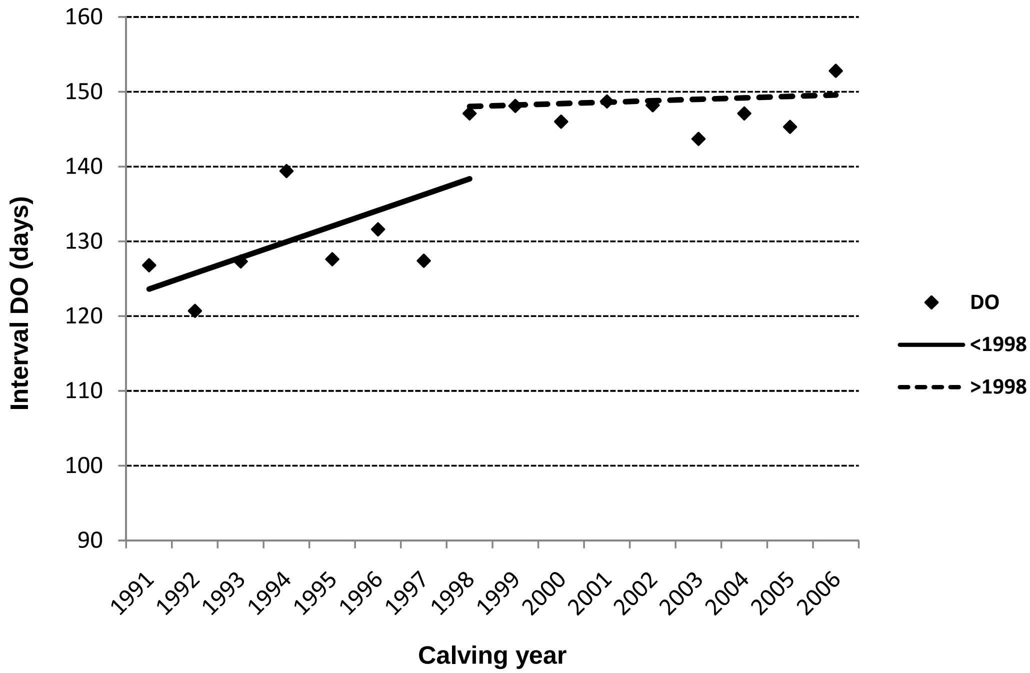

Figure 3.6 The interval from calving date to conception date (days open, DO) for all cows in 14 Holstein herds as affected by calving year.

Overall, the number of days from calving to conception increased from 127 in 1991 to 153 days in 2006. The average DO for 2007 of 135 days was not included in Figure 3.5 because of a smaller number of records of cows being confirmed pregnant. The linear trend (P<0.01) was 1.84 days per year from 1991 to 2006. The largest increase occurred (P<0.10) from 1991 to 1998 at 2.1 days per year, while from 1998 onwards there was no change in the number of days from calving to conception. From this it seems that farmers have adopted a specific strategy pertaining to the voluntary waiting period and insemination protocols to maintain a DO of about 147 days. This would, however result in extended lactations because of longer calving intervals. This could result in a lower lifetime performance; although, the persistency of milk production would reduce this effect. Based on a study done by Washburn *et al.* (2002) it was reported that the number of DO increased from about 126 days in 1976 to 169 days in 1999 for 532 Holstein and 29 Jersey herds in 10 Southeastern states of the United States.

Parity had a significant (P<0.05) contribution to the total sum of squares for days from calving to conception. The average days open for cows in first lactation increased from 136±2 days for first lactation cows to 145±4 days for cows in sixth lactation. This increase was on average 1.5±0.6 days per parity, but varied over time. The average increase, between parity one and four, was 0.22±0.52 days open per parity. From parity 4 to 6, days from calving to conception increased with 3.93±1.81 days per parity. A possible explanation for this trend is that dairy producers may give more insemination opportunities to high yielding cows to conceive and may deliberately delay inseminations after calving for these cows.

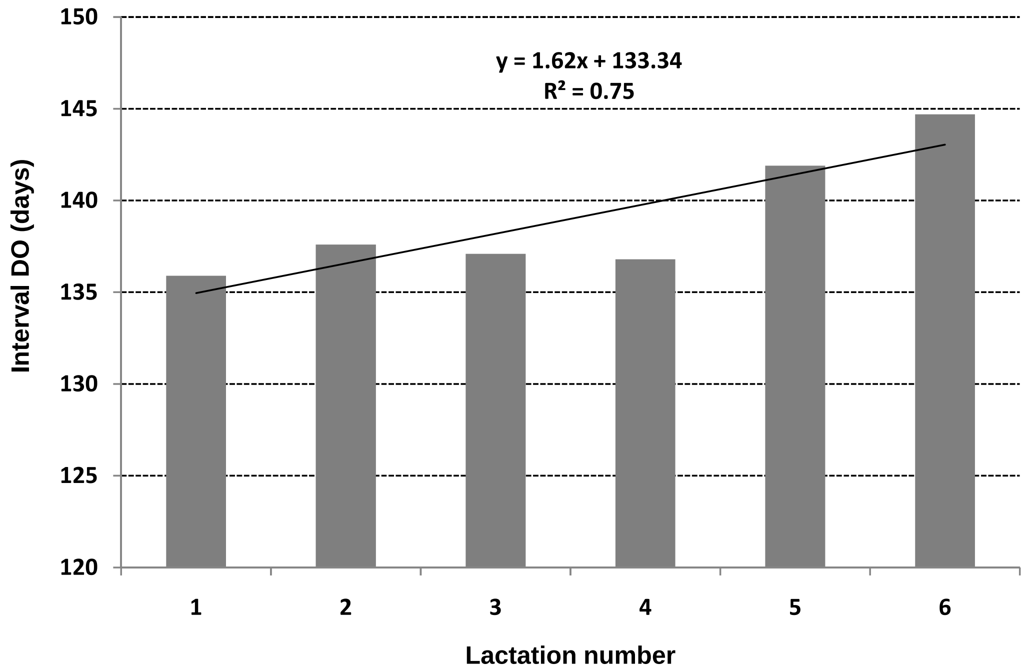

Figure 3.7 The change in the number of days from calving to conception (Days open, DO) for all cows in 14 Holstein herds as affected by lactation number.

Season of calving affected the interval between calving and conception (DO) significantly (P<0.001: Figure 3.8); although, the absolute difference in the number of days was small. Cows calving from October to December had the highest number of days open, i.e. 142 vs. 138 days for the other season of the year. The number of days open is strongly linked to the interval from calving to first insemination, which could be related to the environmental conditions on farms during summer. Cows calving from October to December had the largest (P<0.001) average number of days from calving to conception (142.3±2.0), whereas cows that calved during April to June had the least (P<0.001) average number of days open (136.6±2.0).

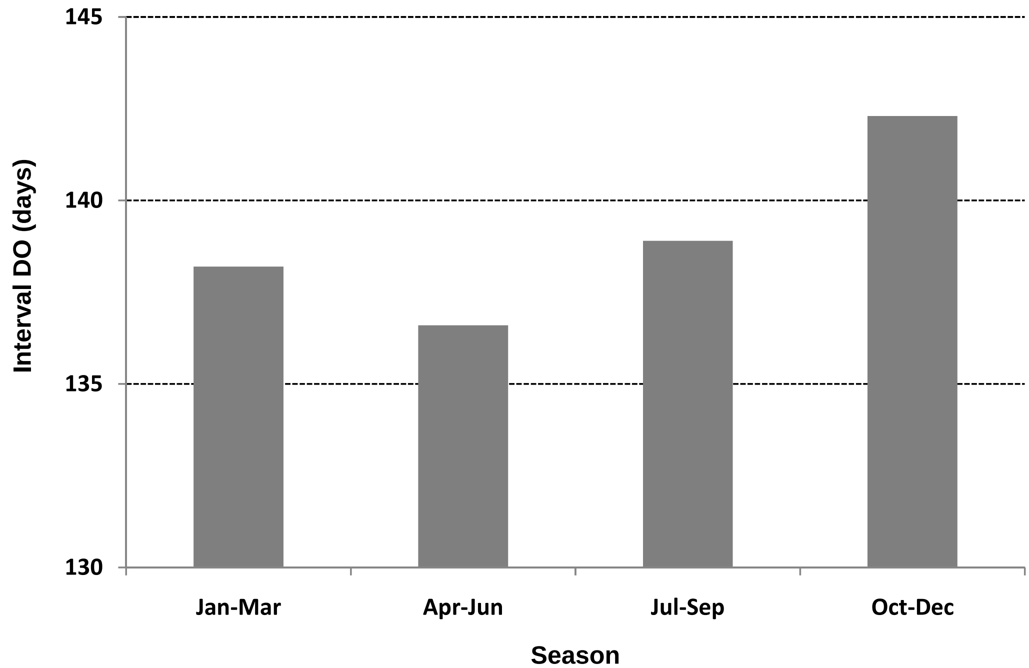

Figure 3.8 The change in the interval from calving to first service for all cows in 14 Holstein herds as affected by season of calving.

Such differences could have been caused by failure of farmers to detect heat after calving; as a result the interval from calving to first service was prolonged, and eventually influencing DO. The significant effects of period ($P<0.001$) and season ($P<0.05$) of calving on days open shown in Table 1 was also reported by Carmona Solano & Sato Vergas (1987) and Mangurkar *et al.* (1985). Cows that calved from 1985 to 1990 had the longest days open (224 days), while those that calved from 1995 onwards had the shortest days open (159 days). Such findings reflect the improvement in the reproductive management by farmers. Also poor quality feeds obtained during the dry periods resulted in longer days open for cows that calved during those periods, because animals take a longer time to recover after calving.

3.4.1.3 Number of services per conception (SPC)

The number of services per conception among herds varied from 1.9 to 3.3 (Figure 3.6) with seven herds showing insemination efficiency figures of below 40%, i.e. the average number of services per conception being higher than 2.5.

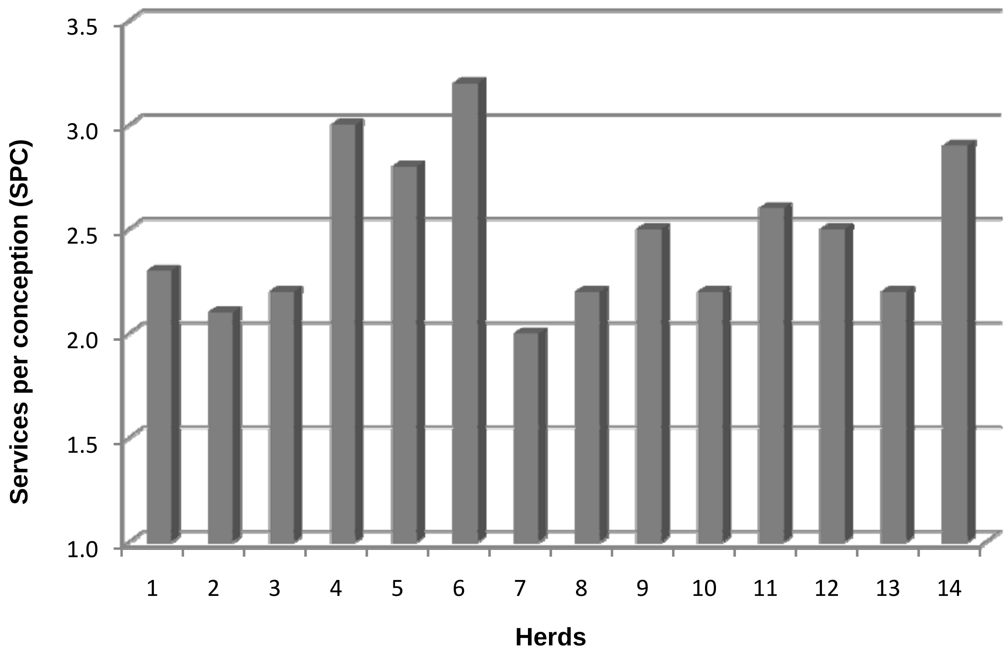

Figure 3.9. The average number of services per conception for all cows in 14 Holstein herds

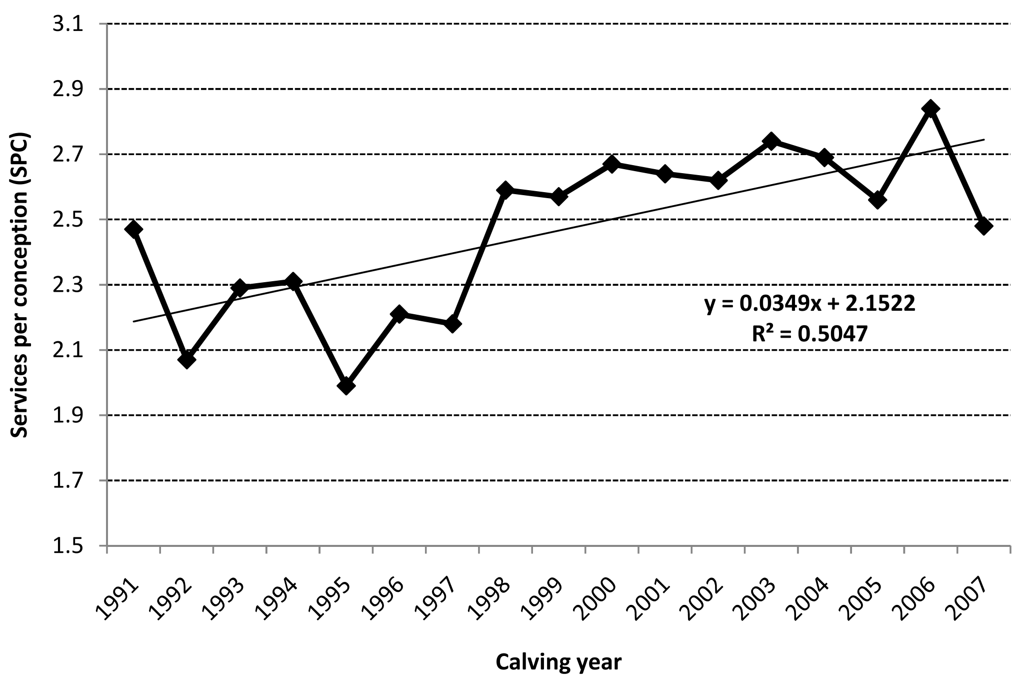

Figure 3.10 The number of services per conception for all cows in 14 Holstein herds as affected by calving year

The number of services per conception as affected by production year is presented in Figure 3.7. A clear linear trend (P<0.01) is observed from 1992 to 2006 with average number of services per conception increasing from 2.1 to 2.9. Specifically from 1998 onwards the number of services per conception was consistently more than 2.5, indicating an insemination efficiency below 40%.

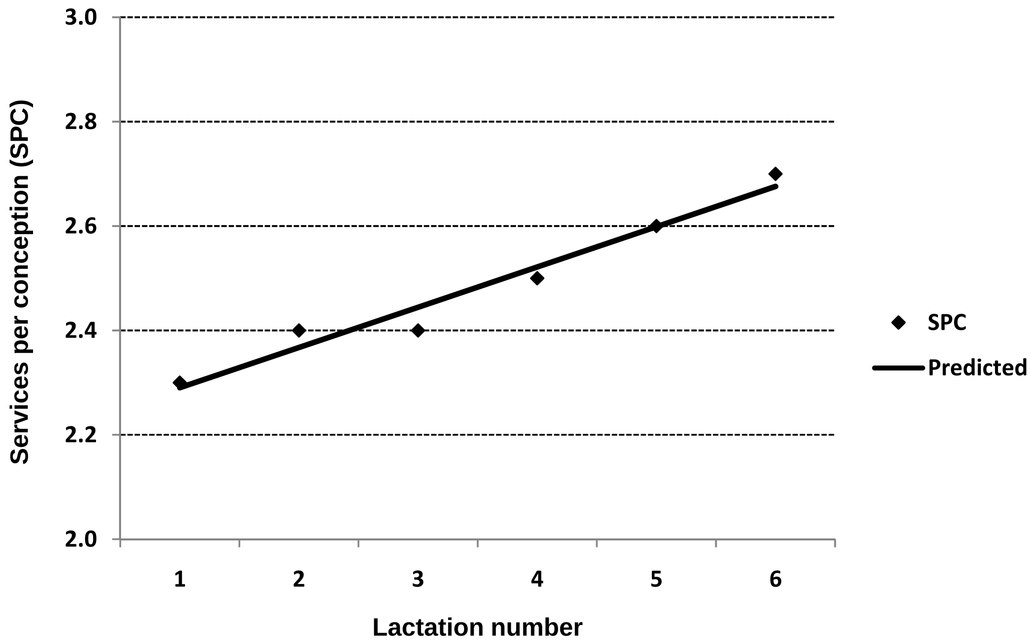

Figure 3.11 The number of services per conception (SPC) for all cows in 14 Holstein herds as affected by lactation number (SPC = 2.21 + 0.08x; R^2 = 0.96)

The number of services per conception increased linearly ($P<0.01$) with an increased lactation number (Figure 3.11). This trend could probably be related to an increasing milk yield for older cows. According to an Australian survey (Little, 2003), farmers would experience reproduction problems in their herds with an average SPC of above 2.32. In the present study SPC was higher than 2.3 in more than 50% of herds. Jamrozik *et al*. (2005) found that number of services (NS) for first parity and older Holstein cows in Canada was 1.64±1.09 and 2.14±1.50, respectively. In the latter analysis, actual NS per conception higher than 10 was assigned to 10. This would have reduced the mean values indicating better reproductive performance by dairy farmers.

A survey by Mackey *et al*. (2007) of 19 Irish Holstein-Friesian dairy herds showed that fertility performance was generally poor with the interval to first service being 84.4±35.4 days and the first insemination success rate 40.6±0.7%. The 100-day in-calf rate was 46.0±0.68% and CI 404±65 days. By back-calculation, i.e the difference between CI and gestation length (González-Recio *et al*. 2006), the number of days open could be calculated at *ca*. 124 days, which is slightly lower than that observed in the present study (134±74 days). Mackey *et al*. (2007) also noted that the major cause of the poor reproductive performance in Irish dairy herds was the prolonged interval to first service and the poor success rate at first AI. The result of this is that only 46% of cows were confirmed pregnant by 100 days-in-milk, although this varied considerably between herds, i.e. from 16.4 to 70.8%. In the present study first AI success rate varied from 24 to 50% between herds. Other researchers (Royal *et al*., 2000; Grosshans *et al*., 1997) found first AI success rates of respectively 39.7 and 48.5%.

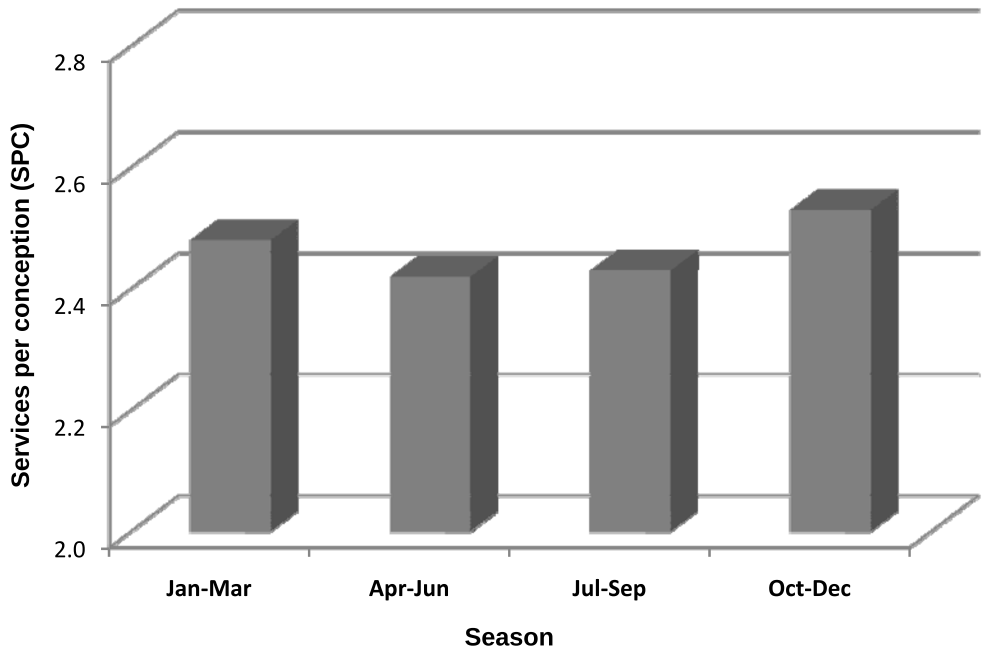

Figure 3.12 The number of services per conception for all cows in 14 Holstein herds as affected by season of calving.

The number of services per conception was lower during the cooler months of the year, i.e. April to September, with a generally higher number of services per conception observed in the summer, i,e, from October to March. These results are consistent with those for the interval from calving to conception (DO) as presented in Figure 3.8.

3.4.1.4 First service within 80 days post-partum (FS80d)

The percentage of cows receiving a first service within 80 days post-partum varied from 39 to 93% for Herd 11 and Herd 14 respectively (Figure 3.13). Over all herds, on average, 64% of cows were inseminated for the first time within 80 days post-partum (Table 3.1). A voluntarily waiting period (VWP) of 21 days was used for all herds as it was not possible to determine a constant reliable VWP for all cows in the dataset. The average interval from calving to first insemination varied from 57 to 100 days (see Figure 3.1).

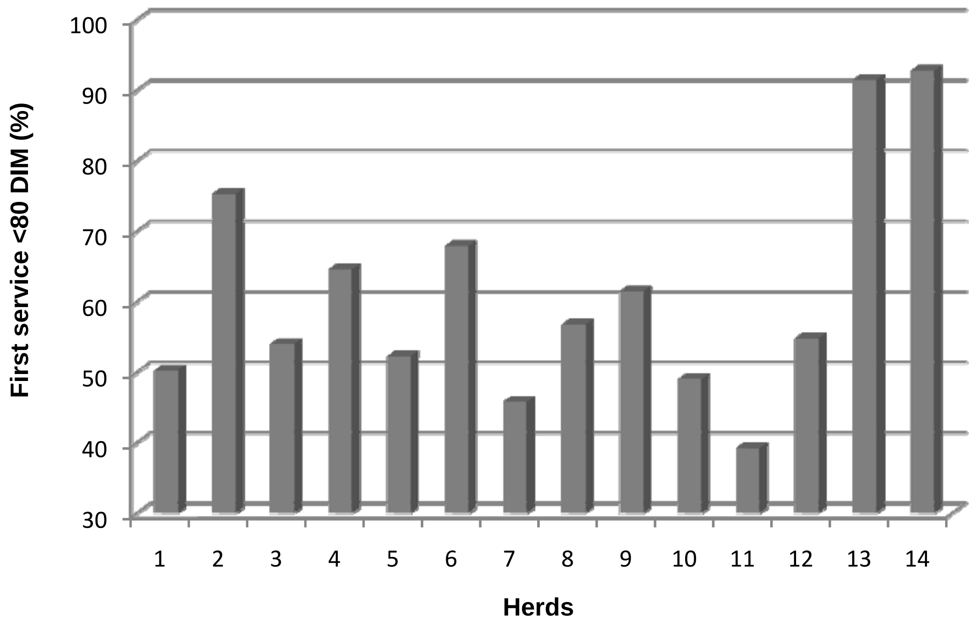

Figure 3.13. The percentage of first services conducted within 80 days post-partum (80 DIM) for 14 Holstein herds

The percentage of cows inseminated within 80 days post-partum decreased from 77% in 1991 to 56% in 2007, i.e at 1.21% per annum (Figure 3.14) with very low values, i.e. 49 and 50% in 2001 and 2002 respectively. Between 1991 and 1994, the percentage of cows serviced within 80 days post-partum decreased by 5.6% per annum, but started to increase marginally by 2.5% per annum from 1994 to 1998. A significant reduction in FS80d was experienced from 1998 to 2002, i.e from 64% to 49%. From 2002 to 2003 FS80d increased from 49.8 to 61.9% and since 2003 to 2007 decreased from 61.8 to 56.4%, i.e at 1.10% per annum.

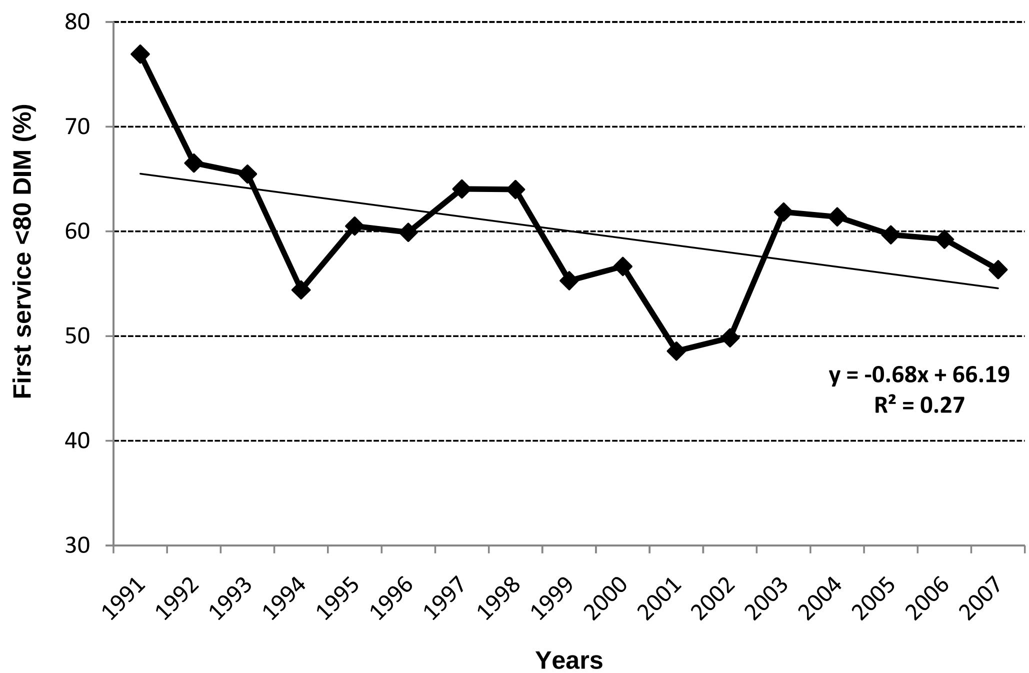

Figure 3.14 The percentage of first services conducted within 80 days post-partum (< 80 DIM) for all cows over all lactations in 14 Holstein herds as affected by calving year.

The percentage of cows serviced within 80 days post-partum increased with parity from 56% for first lactation cows to 62% for third and fourth lactation cows (Figure 3.15). A second degree polynomial regression equation (y $-0.831x^2 + 5.927x + 51.673$; $R^2 = 0.90$) described the data best. Although the regression equation is significant ($P<0.01$), actual values varied little for cows in different lactations. This is, however, a positive indicator as there is a general perception among dairy farmers that older cows (who usually produce more milk) would be more difficult to show heat soon after calving. Data from this study does not support that contention.

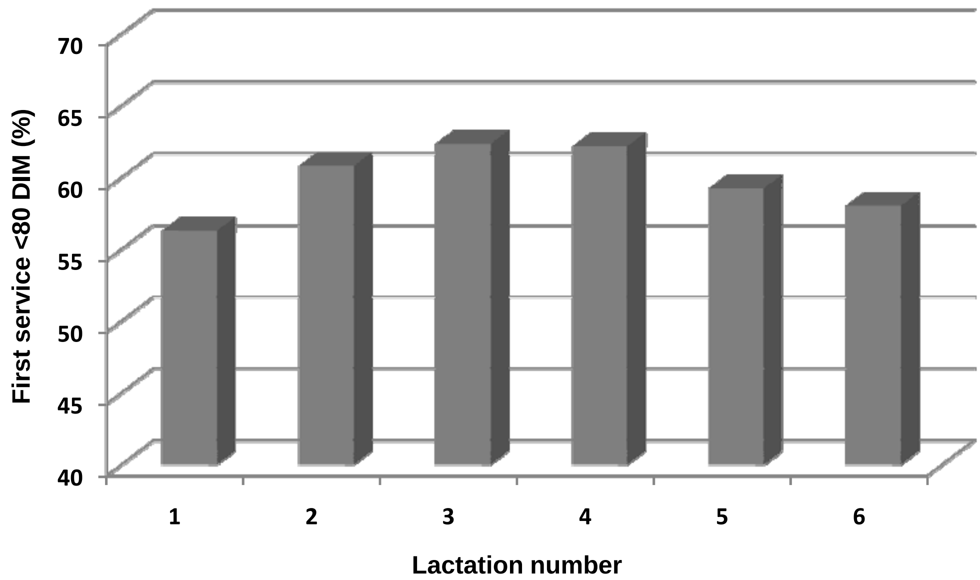

Figure 3.15 The percentage of first services conducted within 80 days post-partum (<80 DIM) for all cows in 14 Holstein herds as affected by lactation number

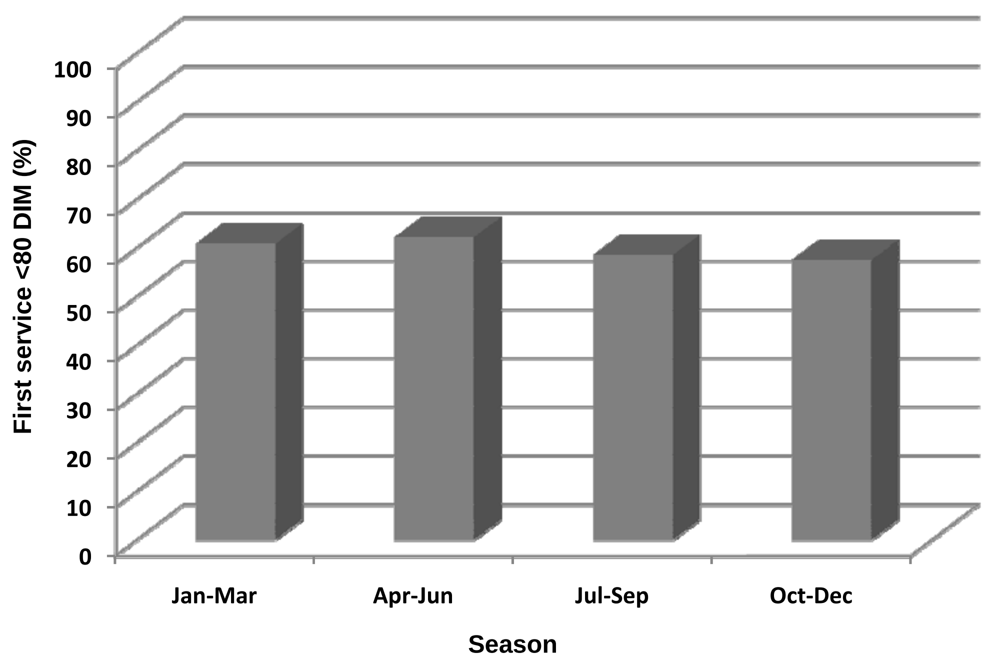

Figure 3.16 The percentage of first services conducted within 80 days post-partum (<80 DIM) for all cows in 14 Holstein herds as affected by season of calving.

The percentage of cows inseminated within the first 80 days post-partum is presented in Figure 3.16. Observed values varied little between seasons - minimum and maximum percentages were 58 and

62% - indicating that although seasonal effects were small, it was significant (P<0.01). It is expected that early first inseminations would be lower during the summer months because of the general perception that cows experience poor fertility during the hot time of the year, however, data from this study do not support this assumption.

Significant seasonality in reproductive performance of dairy cows exists in Southern Africa. According to Lopez-Gatius (2003), significant decreases in cyclicity and services per conception were reported during warmer summer months, compared with cooler winter months in 4 herds between 1991 and 2000 in Spain. The effect of season on FS80d was significant. Cows that calved during season 1 and 2 (January – June) had the highest rate of FS80d, i.e 61 and 62%. As opposed to season 1 and 2, FS80d for cows that calved during season 3 and 4 (July – December) were respectively 59 and 58%. Some dairy producers deliberately do not breed cows during parts of the summer (Washburn *et al*., 2002; Oseni *et a*l., 2003). Fertility of dairy cows is reduced under heat stress during hot summer months (Jordan, 2003) and delayed breeding may be economically advantageous under certain conditions (Grohn & Rajala-Schultz, 2000; Arbel *et al*., 2001).

3.4.1.5 Cows confirmed pregnant within 100 (PD100d) and 200 (PD200d) days post-partum

The percentage of cows confirmed pregnant within 100 and 200 days post-partum, as affected by herd, is presented in Figure 3.17. Percentages differed between herds with a minimum and maximum percentage PD100d ranging between 14 and 45% respectively. Deliberate changes in reproductive management could explain some of the differences observed between herds. Many dairy producers may have increased their VWP past 70 days because studies showed increased conception rates after longer VWP (Britt, 1985).

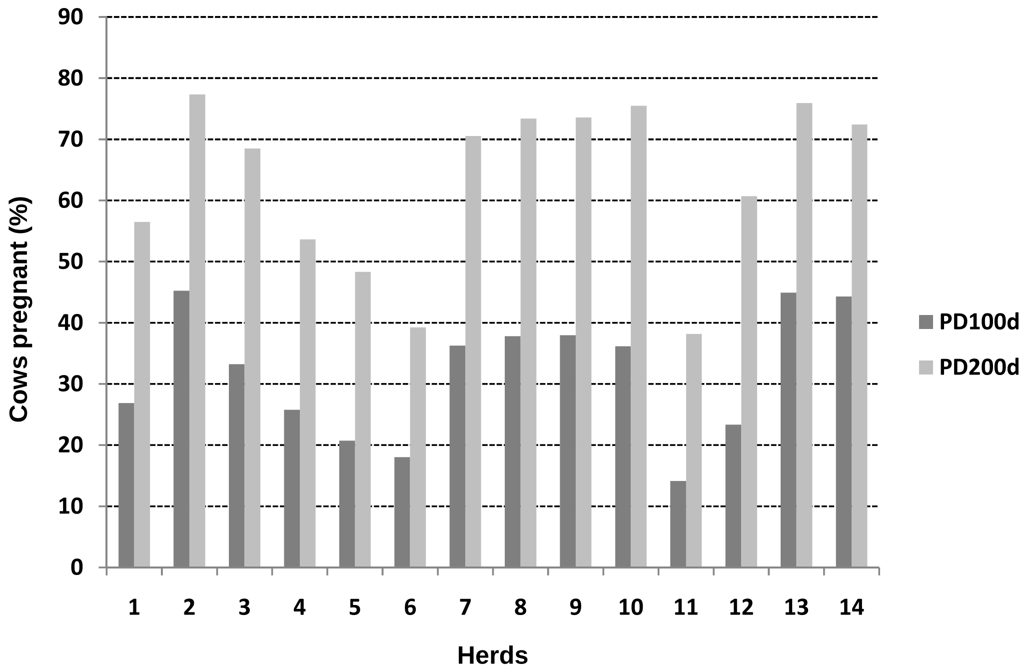

Figure 3.17. The percentage of cows confirmed pregnant within 100 (PD100d) and 200 (PD200d) days post-partum for 14 Holstein herds

The percentage of cows confirmed pregnant within 100 and 200 days post-partum as affected by calving year is presented in Figure 3.18. While the percentage of cows confirmed pregnant within 100 days post-partum decreased ($P<0.05$) from 44 % in 1991 to 27% in 2007, this was not observed for cows confirmed pregnant 200 days post-partum. Numerically fewer cows were confirmed pregnant by 200 days post-partum in 2007 in comparison to 1991, i.e. 68 vs 55%. The linear trend for this trait was not significant ($P>0.05$) probably because of large variation between years. The unexpected behaviour of this trend in year 1994 for cows was probably due to a smaller number of animals with records available in the data set for that particular year.

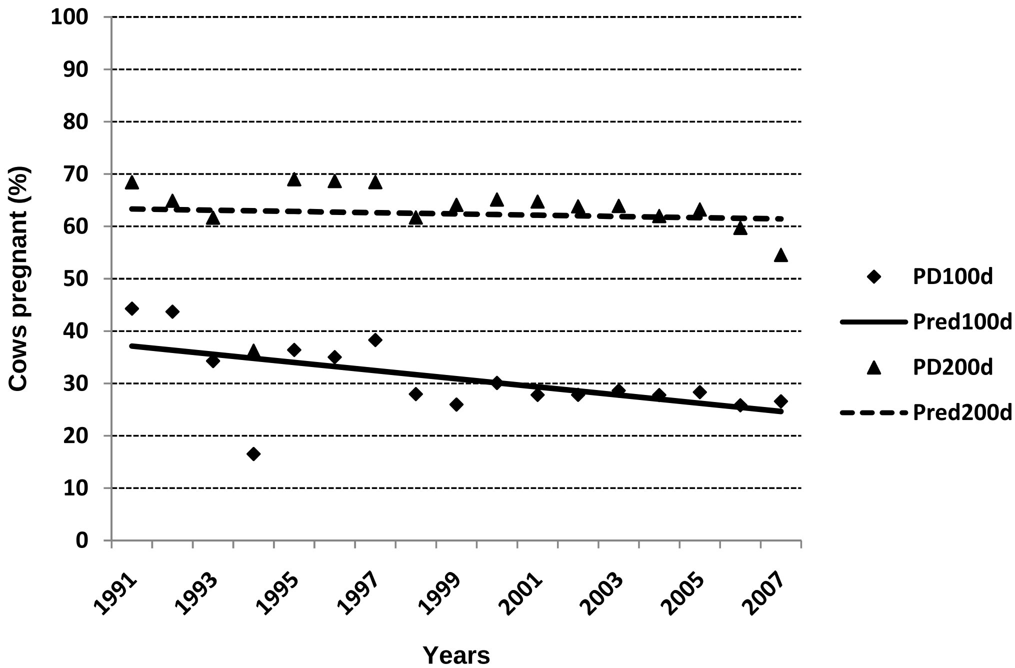

Figure 3.18 The percentage of cows confirmed pregnant with 100 (PD100d) and 200 (PD200d) days post-partum for all cows in 14 Holstein herds as affected by calving year.

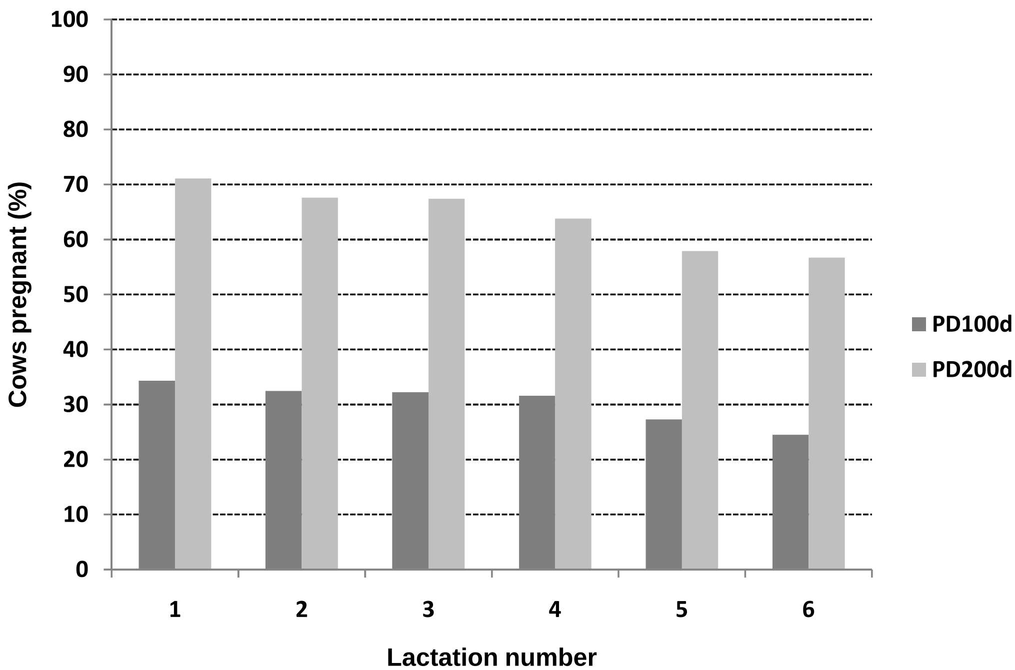

Figure 3.19 The percentage of cows confirmed pregnant with 100 (PD100d) and 200 (PD200d) days post-partum for all cows in 14 Holstein herds as affected by lactation number.

The percentage of cows confirmed pregnant within 100 and 200 days post-partum decreased linearly (P<0.01) from parity one to parity six. For PD100d the reduction in the percentage of cows confirmed pregnant showed a polynomial trend because the reduction in the percentage of cows confirmed pregnant was relatively small from first to fourth lactation in comparison to the subsequent reduction to sixth lactation.

The percentage of cows confirmed pregnant after 100 and 200 days post-partum differed between season of calving (Figure 3.20) Cows that calved from January to September showed higher percentages of pregnancy 100 days post-partum than cows that calved from October to December. As mentioned previously, some dairy producers deliberately do not breed cows during parts of the summer (Washburn *et al.,* 2002; Oseni *et al*., 2003).

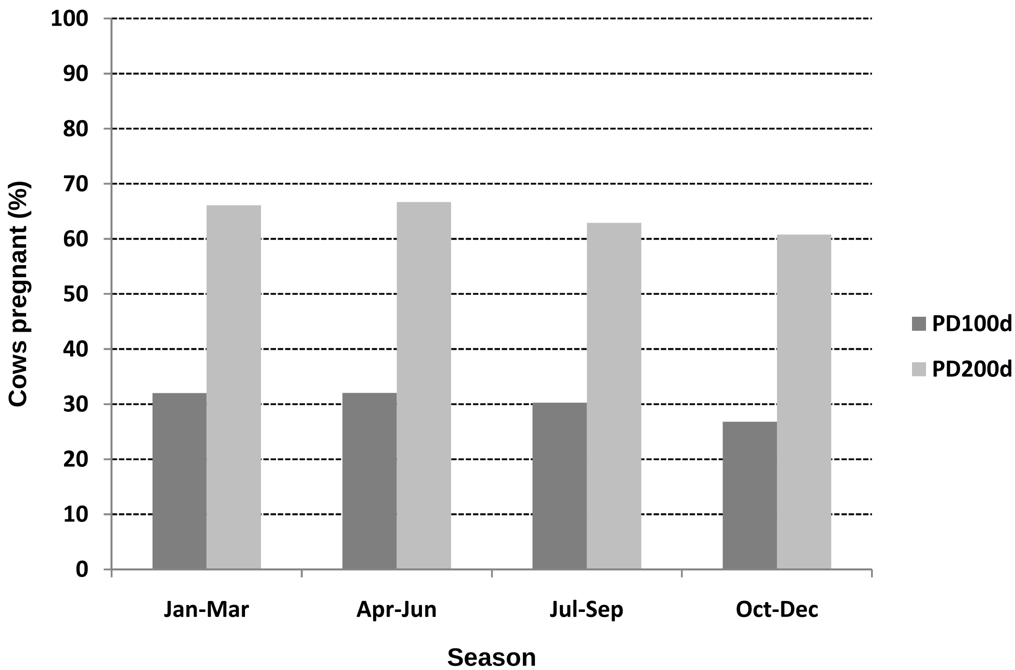

Figure 3.20 The percentage of cows confirmed pregnant within 100 (PD100d) and 200 (PD200d) days post-partum for all cows in 14 Holstein herds as affected by season of calving.

3.4 CONCLUSION

Culling policies affect the profitability of the herd and can have a significant impact on the reproductive statistics (Plaizier *et al*., 1997, 1998). High levels of aggressive culling may not, however, be an economically optimal approach. Voluntary culling offers an opportunity for improvement of the genetics and profitability of the herds by removing low producing animals. Involuntary culling, on the other hand, is forced due to disease problems or reproductive failure and is typically detrimental to the profitability (Dijkhuizen *et al*., 1985; Esslemont, 1992; Rajala-Schultz *et al*., 2000a). Allaire and

Cunnignham (1980) estimated that maximum profits occurred when about 20–23% of the herd was replaced annually and Rajala-Schultz et al. (2000b) reported that the maximum expected net returns for a herd occurred when total replacement percentage of about 25–26%.

This study provides an initial analysis of the standard of reproduction management in South African Holstein herds. Reproduction traits were significantly affected by herd, calving year, calving season and lactation number. Interval traits showed an increase over time; although it reached a plateau of 80 days for the interval C-1stAI and 140 days for DO, probably indicating a large management effect on these interval traits. Genetic parameters will be estimated for these fertility traits in order to provide an indication of a genetic effect on reproduction performance. It is important to conclude that all these fixed effects modeled affected the reproduction traits under consideration. It is thus important to include them in statistical models for estimating genetic parameters, as the parameters will otherwise be biased.

CHAPTER 4

GENETIC PARAMETER ESTIMATES FOR SOME FERTILITY TRAITS IN SOUTH AFRICAN HOLSTEIN DAIRY COWS

4.1 Abstract

Genetic parameters for fertility traits would give an indication of the response to selection in dairy cattle herds. In this study, genetic parameters for and correlations among fertility traits, sourced from standard reproduction management data bases, were analysed for Holstein cows using Gibbs sampling. Insemination events (n = 69 181) from 26 645 lactations of 9 046 Holstein cows from 14 herds, calving down between 1991 and 2007, were available. The outcome of each AI event was known. Insemination records were linked to the calving date of each cow, lactation number as well as dam and sire identification numbers. Fertility traits indicating the ability of cows to show heat early in the breeding period, and to become pregnant, were derived. Heritability estimates ranged from 0.04±0.01 to 0.10±0.02 for First Service within 80 days (FS80d), from 0.07±0.01 to 0.08±0.02 for Pregnant Following Insermination after 100 days post-partum (PD100d) and from 0.06±0.04 to 0.08±0.02 for Pregnant Following Insermination after 200 days post-partum (PD200d) depending on the specific two-trait combination. Although heritability estimates of most fertility traits were below 0.10, they were in close agreement with estimates published by other researchers using linear models. Genetic correlations between different fertility parameters analyzed in this study indicated that there is not likely to be a single characteristic that would serve well for selection purposes; however, combining different traits could be considered in selection programmes to improve fertility. Further research in constructing an optimal fertility index is warranted.

4.2 Introduction

The main objective of dairy producers is to maximize returns on milk production while minimizing input costs (Freeze *et al*., 1992). This approach forces dairy producers to maintain minimum reproductive performances while still managing high milk production levels. The consequences of reproductive problems are extended lactations, a higher number of inseminations, higher veterinary costs, and more involuntary culling of normally productive cows. However, long-term selection for milk yield in dairy herds has caused deterioration in some non-production or "secondary" traits as a result of antagonistic genetic relationships. As a result, more cows are being culled involuntarily as a consequence of poor fertility (Hansen *et al*., 1983; Weller, 1989; Lopez-Gatius *et al*., 2002). Poor on-farm fertility can partially be addressed by management changes (improved feeding, better heat detection, etc.). These management changes require continuous inputs and therefore attract continuous costs, suggesting that this route to improved fertility is unsustainable in the long term. Ignoring the genetic component of poor fertility masks the severity of the problem. A failure to address the genetic component of poor fertility is expected to lead to a continuing downward genetic trend. Genetic selection may provide a cost-effective, cumulative, and permanent method for improvement of fertility in the national South African dairy herd.

The reproductive performance of dairy cow consists of an array of several traits. These traits are observed around each pregnancy, starting as a heifer. Fertility could therefore be observed repeatedly as the cow ages until she is culled because of not becoming pregnant. Fertility can change with the age of cows, often depending on previous performance (Jansen *et al*., 1987). Improving the genetic merit of cows for fertility is difficult as the heritability estimates of most reproductive traits are generally below 0.10 (Wall *et al*., 2003; Kadarmideen *et al*., 2003). This implies that the environment has a large effect on the fertility performance of dairy cows. Even though heritabilities were quite low, the additive genetic variation from these traits is deemed to be sufficient to allow effective selection (Weller & Ron, 1992; Boichard & Manfredi, 1994; Weigel & Rekaya, 2000).

Although the heritabilty of fertility is low, ranging from 1 to 10% depending on the definition of the trait and the methodology used for its analysis, there is a consensus that sufficient genetic variability exists, and this can be exploited to improve reproductive performance. Several types of traits are used in fertility evaluation, ranging from binary (discrete) responses to continuous or interval traits. Genetic evaluation of fertility is difficult, mainly because of incomplete data recording and lack of proper statistical methods for handling discrete, skewed, and censored observations. Consequently, depending on the trait definition, different models and methodologies have been implemented to analyze reproductive performance. Even though direct recording of fertility in national milk recording schemes is generally more open to measurement error and is less widespread, fertility traits are genetically correlated with traits that are either well recorded or with a higher heritability, such as milk yield, body condition score (Pryce *et al*., 2000), birth weight (Berry *et al*., 2003), and linear type traits (Harrison *et al*., 1990). As a result, direct measures of fertility (days open, calving interval, insemination data) and records on correlated traits, such as milk yield and body condition score, can be used to supplement the predictions of genetic merit for fertility. The use of production traits and body condition score is beneficial because they can help to overcome management biases that may be present in the fertility data. The correlation between milk yield and fertility is not unity; therefore, a favourable selection response in fertility can be achieved while still achieving gains in milk production.

According to Kadarmideen *et al.* (2003), characters of good cow fertility can be defined as cows that show visible signs of heat at the right time after calving (days to first heat or first insemination) and that conceive when inseminated the first time (success of conception to first service). This definition addresses two important reproductive phenomenon: cyclicity and the ability of cows to conceive. When these criteria are met, other fertility measures such as days open and calving interval will then take their normal biologically determined values.

Variation in the number of services per conception (SPC) reflects variation in female fertility, and the trait gives a measure of pregnancy rate directly (González-Recio *et al*., 2004). The number of services per conception (SPC) is closely related to the goal of improving fertility and has a clear economic interpretation. SPC suffers from the same limitations as CI, in that it is necessary to have a consecutive calving date, and relies on consistent recording, as all inseminations need to be recorded. A high SPC results in prolonged days open (DO), and increased feeding, insemination, and culling costs, as well as a delay of onset of subsequent lactation. In turn, DO is an interval trait, and a composite measure of time to first insemination and of pregnancy rate (González-Recio & Alenda, 2005). DO can provide information about fertility supplementary to SPC. Thus, DO is a widely used trait for assessing female fertility in dairy cattle (Dematawewa & Berger, 1998; Van Raden *et al*., 2004). However, DO depends heavily on management practices, because a longer voluntary waiting period before insemination may be preferred for high-yielding cows (Dekkers *et al*., 1998). Dematawewa & Berger (1998) found strong positive phenotypic and genetic correlations between days open (restricted to a maximum of 305d) and total number of breeding opportunities (varying from 1 to 9) during each lactation using linear animal models. Roxström *et al*. (2001) reported a genetic correlation (0.73) for days from calving to last insemination with number of inseminations, also using a linear model. Jamrozik *et al*. (2005) reported genetic correlations of 0.92 and 0.96 between number of services and intervals from first service to conception (FSTC) for first and later lactation cows, respectively.

A concern in the genetic analysis of fertility is how to handle cows that do not become pregnant or that are culled with unknown pregnancy status (i.e. censored records). There are few estimates of the genetic correlations between STC and DO probably due to censoring acting on both traits; that is, cows are culled before the next calving with unknown pregnancy status. Ignoring censoring can distort inference and produce biased estimates of genetic parameters (Carriquiry *et al*., 1987). Loss of information due to incomplete records can be reduced if censoring is considered in genetic analysis.

Calving interval (CI) has a relatively high economic weight (Groen *et al*., 1997), and a reduction in CI could be described as one of the outcomes of improved fertility. However, CI requires a record of two consecutive calving dates and is therefore only available after a second calving. Relying on CI alone would delay selection decisions. Moreover, CI is open to management bias (e.g., decisions to extend the lactation length of individual high-yielding cows within herds). Early measures on components of CI can be useful in overcoming some of these problems. For example, days to first service (DFS) are available much earlier and have been shown to be heritable (de Jong, 1997; Evans *et al*., 2002) and strongly correlated to CI on the genetic level (de Jong, 1997).

Kadarmideen & Coffey (2001), in an analysis of U.K. insemination data, showed that only about 10% of herds that participate in herd milk recording had all the expected service dates, and over 15% of herds failed to record almost all services. Missing records occur for different reasons (e.g., inseminations not being recorded by the producer or the producer failing to report all successful or unsuccessful services to milk recording institutions). Because of these characteristics of insemination data, careful editing is required before insemination data can be used to derive fertility proofs (Kadarmideen & Coffey, 2001).

Kadarmideen *et al*. (2000) estimated genetic parameters for various disease resistance traits and conception after first insemination in the UK dairy population using linear and threshold models. They concluded that threshold model yields slightly higher estimates.

Not all sources of variation are accounted for in many fertility analyses, particularly when only one record per cow is used. Weigel (2000) reported that almost 50% of the usable data is discarded by considering only first services, because at least half of the cows have repeated insemination data available. The same author concluded that the use of such additional information is desirable. Furthermore, a high proportion of the fertility data is usually discarded as a result of inconsistencies in data recording that necessitate stringent editing. Thus, including the repeated records will increase the quantity of information, leading to more accurate fertility evaluations.

Determining which traits to include in a genetic evaluation for fertility is difficult. Previous studies on cow reproduction had only calving dates from which calving intervals or days open could be computed, assuming a standard gestation length (Jansen, 1986). This assumption has not always been correct because of possible differences in gestation length between different service sires. The availability of insemination data has allowed the calculation of interval traits, as well as the number of inseminations. Age at first calving and the intervals from calving to first service and first service to conception in each lactation have been important traits in several studies.

Fertility is a complex trait and the challenge is to decide which traits are to be considered in genetic evaluations for fertility, due to low heritability, and to its unfavourable correlation with milk yield. Environmental factors were found to have a large effect on fertility traits (Hayes *et al*., 1992). Herd management, year of calving, season/month of calving and parity were all factors that affected fertility in different studies (Thaller, 1997).

In this study, traits obtained from standard reproduction management data sources, are analysed using bivariate linear-linear and linear-threshold animal models to estimate genetic parameters and to correlate traits to identify suitable traits for improving the fertility in South African Holstein cows.

4.3 Materials and Methods

4.3.1 Data

Data on insemination and calving events (n = 69 181) of 14 South African Holstein herds, from 1991 to 2007, were obtained from a dairy herd farm reproduction management software programme (DIMMSA), developed for the Holstein industry (Cloete, S., personal communication). A total of 24 646 lactation records from 9 046 individual cows was available. The outcome of each AI event was known. Insemination records were linked to the calving date of each cow, lactation number, dam and sire identification numbers. By using this information, fertility traits indicating the ability of cows to show heat early in the breeding period were derived. The probability of the success of each insemination and confirmation of pregnancy were also derived. These fertility traits were defined based on data availability in a way that they would describe a complete picture of the reproductive history for the cows. Before analyses, records with missing sire and dam identification numbers were removed from the data set. After further edits, a data set of 16 648 records was suitable for analyses. Several authors (Pryce *et al.* 1998) have required that all cows have a subsequent calving date. This restriction was not implemented in the present study, because including only those cows that eventually became pregnant could introduce selection bias.

4.3.2 Statistical analysis

The data were analysed using bivariate linear-linear and linear-threshold animal models. The fixed effects fitted were herd (14 levels), year (17 levels), season (4 levels) and lactation number (6 levels). The traits analysed were interval from calving to first service (CFS), interval from calving to conception (DO), number of services per conception (SPC), (all linear) and as binary traits (coded 1=no and 2=yes) whether cows were inseminated for the first time within 80d post-partum (FS80d), whether cows were confirmed pregnant within 100d post-partum (PD100d) and whether cows were confirmed pregnant within 200d post-partum (PD200d).

The model included the random effects of animal and animal permanent environment (PE). The software used was THRGIBBS1F90 (Misztal, 2008). Single chains of 250 000 cycles were run, with the first 50 000 cycles used as the burn-in period. This was followed by post Gibbs analysis, using POSTGIBBSF90 (Misztal *et al*., 2002) to determine convergence by visual examination of plots of covariance components by iteration (Figure 4.1 and 4.2). Posterior means were used to calculate the heritability and animal PE variance ratios for each trait. Genetic, animal PE and residual correlations were calculated accordingly. The following multi-trait model was therefore implemented:

$$\mathbf{y}_{ijklm} = \mathbf{f}_{ij} + \mathbf{a}_{ik} + \mathbf{c}_{ik} + \mathbf{e}_{ijklm}$$

In this model, **y** was a vector of observations for underlying values for ith threshold or the observed values for the ith linear traittrait; $\mathbf{f}_{ij}$ was the fixed effect j for the i^{th} trait; $\mathbf{a}_{ik}$ was the additive genetic effect of the k^{th} animal for the i^{th} trait; $\mathbf{c}_{ik}$ was the animal permanent environmental effect of the k^{th} animal for the i^{th} trait, and $\mathbf{e}_{ijklm}$ was the vector of randomly distributed residual effects.

Table 4.1 Descriptive statistics for the raw data analysed for the interval from calving to first service (CFS), interval from calving to conception (DO), number of services per conception (SPC), whether cows were inseminated for the first time within 80d post-partum (FS80d), whether cows were confirmed pregnant within 100d post-partum (PD100d) and whether cows were confirmed pregnant within 200d post-partum (PD200d)

Variable	CFS(days)	DO(days)	SPC	FS80d	PD100d	PD200d
Number of records	16 605	14 255	14 255	16 648	16 648	16 648
Mean	77.3	133.9	2.55	0.64	0.36	0.71
Standard Deviation	29.9	74.3	1.79	0.48	0.48	0.45
Coefficient of variation (%)	38.7	55.5	70.2	75.2	133.7	64.0
Min	21	21	1	1	1	1
Max	250	435	8	2	2	2

Bayesian methods have recently emerged as an option for solving problems related to the evaluation of genetic merit in binomial traits for animal populations. In a Bayesian context, the difference between a fixed and a random effect vanishes because all parameters are considered random variables derived from a given distribution function (Pretorious & Van der Merwe, 2000). Bayesian inference is used to derive the joint posterior distribution by application of Bayes theorem. Bayes theorem relates conditional and marginal probabilities. Markov Chain Monte Carlo (MCMC) methods, including Gibbs sampling can be used as a tool for Bayesian inference (Pretorious & Van der Merwe, 2000). The algorithm is based on generating, in sequence, variables from all the full conditional densities. The full conditional density is the density of a variable given to all the other parameters in the model. Gibbs sampling is a stochastic integration procedure used to estimate joint and marginal distributions of all parameters in a model from their full conditional posterior distributions. This method has been suggested for use in animal breeding particularly when data does not fit a normal distribution (Chang *et al*., 2001).

The Gibbs chain of samples does not immediately converge to given samples from joint posterior distribution. A period, known as the burn-in period, is needed during which the sampling process moves from the initial values of the parameters to those from the joint posterior distribution. To avoid possible influences of the starting values, the initial samples are discarded. After the burn-in period all samples are kept for calculating posterior means and posterior standard deviations of the parameters. The length of the burn-in period is normally judged by visually inspecting a plot of sample values against rounds (Sorensen & Gianola, 2002).

To start the iterations, the user has to supply starting values as the initial priors of the process. The nature or the distribution of the priors may influence the inference process. Sorenson & Gianola (2002) showed that the contribution of the prior to the posterior becomes less and less important with increasing sample size. Therefore, given enough data, the prior is expected to have a small influence on inferences about θ. Visual inspections of the trace plots from the outputs of the Gibbs sampler were used to access the number of iterations and the required length of burn-in period. The convergence for the genetic parameters in the bivariate analysis between CFS and PD100d are presented in Figures 4.1 and 4.2.

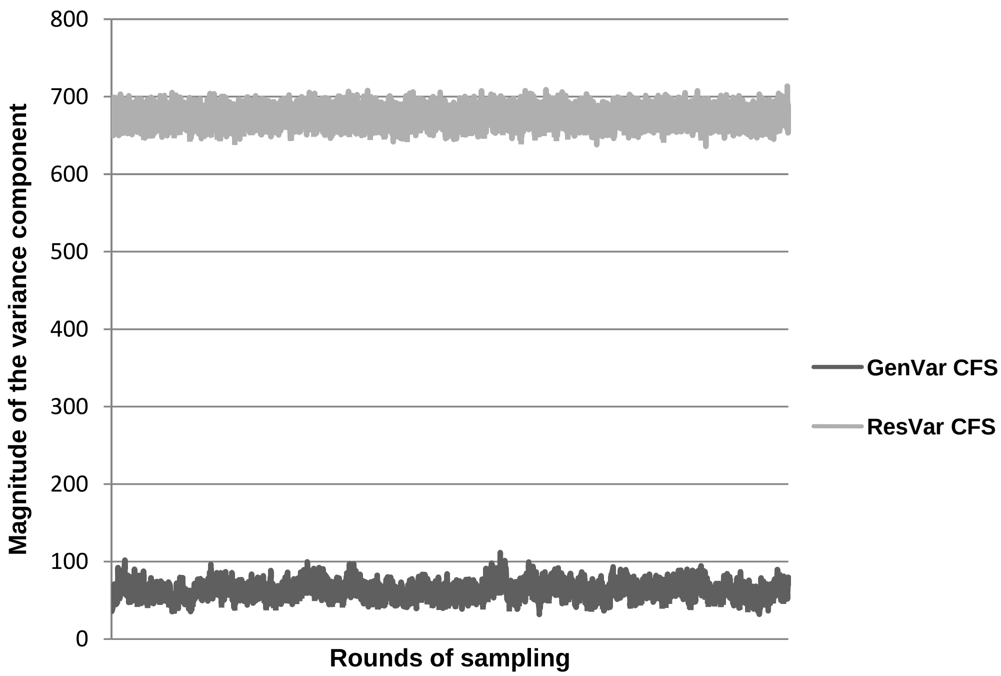

Figure 4.1 Trace plot to establish convergence for the bivariate analysis between CFS and PD100d..

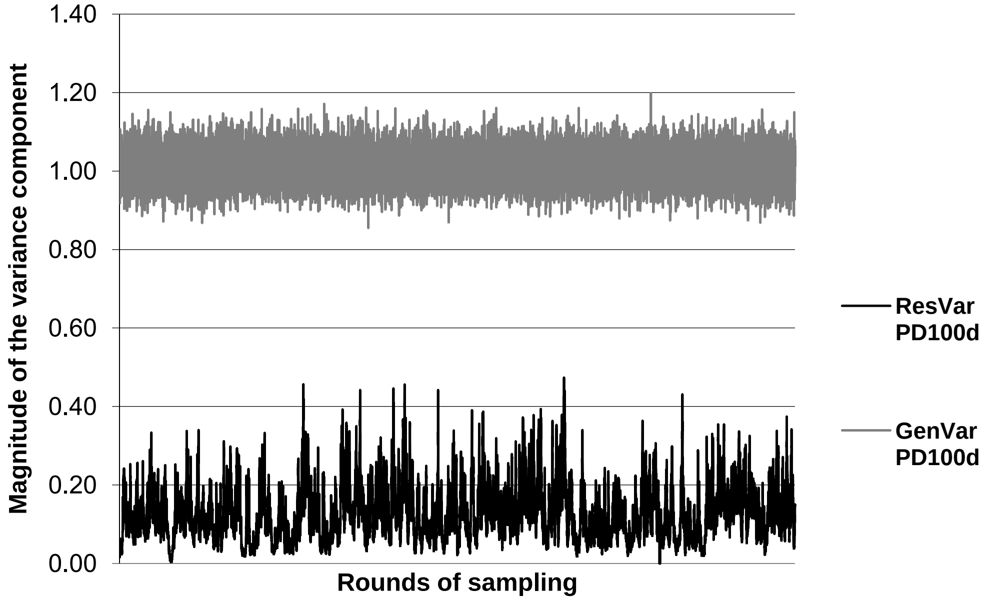

Figure 4.2 Trace plot to establish convergence for the bivariate analysis between the interval between calving and first service (CFS) and PD100d.

4.4 Results and Discussion

Histograms depicting the Highest Posterior Density (HPD) distributions for two of the analysed traits are presented in Figures 4.3 (the linear trait days open) and 4.4 (the categorical trait frequency of cows being pregnant within 100 days post-partum). The difference in skewness of the additive genetic variance distributions for the categorical trait as opposed to the linear trait is clearly demonstrated in the graphs.

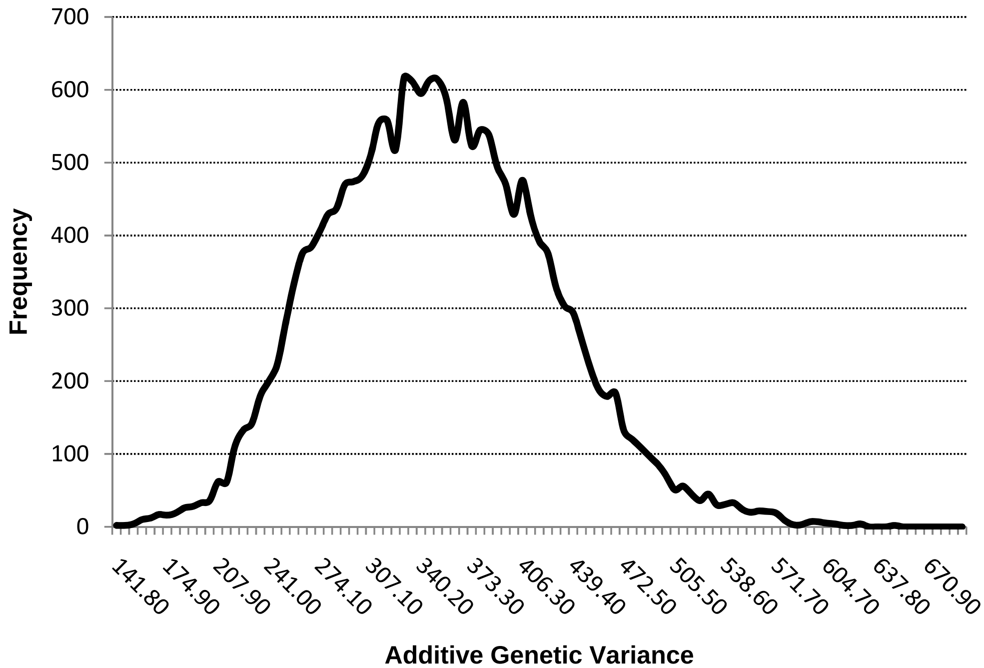

Figure 4.3 Posterior density distribution for the additive genetic variance of the linear trait days open (DO)

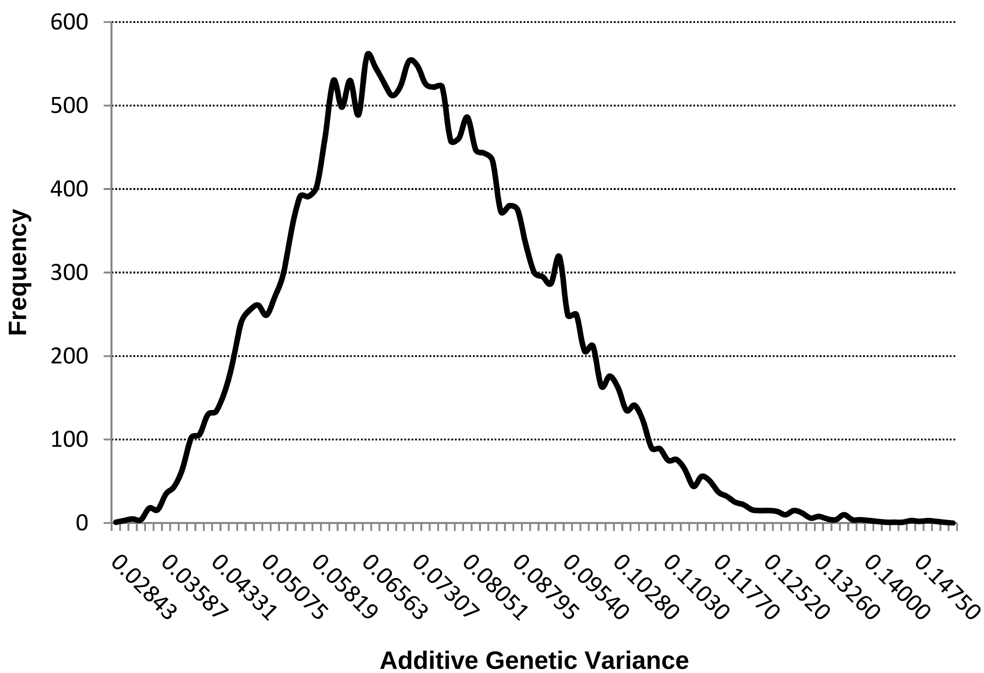

Figure 4.4 Posterior density distribution for the additive genetic variance for the binary trait PD100d (cows pregnant within 100 days post-partum)

Some of the genetic parameters that were estimated using a series of bivariate analyses are reported in Table 4.2. The highest posterior density (HPD) confidence interval for the linear trait FS80d additive genetic variance ranged from a minimum of -0.03928 to a maximum of 0.18160, depending on the two-trait combination. Heritability estimates ranged from 0.04±0.01 to 0.10±0.02 for FS80d depending on the bivariate trait combination. The additive genetic variance (σ_a^2) for the bivariate analyses of FS80d and CFS is very low and this also resulted in the low heritability of 0.04±0.01 for the two-trait analyses of FS80d with CFS.

Table 4.2 Mean (co)variance components, posterior standard density (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios for fertility traits in South African Holstein cows using bivariate linear–threshold analyses

		Correlated threshold trait		
Linear Trait	**Item**	**FS80d**	**PD100d**	**PD200d**
Days Open (DO)	Additive Genetic PSD	0.056340	0.01483	0.04228
	Additive genetic lower HPD	-0.03928	0.04770	-0.01597
	Additive genetic upper HPD	0.18160	0.10580	0.14980
	Additive genetic variance (σ_a^2)	0.07113	0.07675	0.06690
	Environmental variance (σ_e^2)	1.00000	1.00000	1.00000
	Permanent environmental variance (σ_{pe}^2)	0.08110	0.09000	0.1046
	Direct heritability (h^2)	0.06±0.05	0.07±0.01	0.06±0.04
	Permanent environment effect (c^2_{pe})	0.07±0.05	0.08±0.01	0.09±0.04
Calving to First Service (CFS)	Additive genetic PSD	0.01116	0.01948	0.02210
	Additive genetic lower HPD	0.01853	0.05172	0.05537
	Additive genetic upper HPD	0.06227	0.12810	0.14200
	Additive genetic variance (σ_a^2)	0.04040	0.08990	0.09869
	Environmental variance (σ_e^2)	1.00000	1.00000	1.00000
	Permanent environmental variance (σ_{pe}^2)	0.00387	0.06584	0.12560
	Direct heritability (h^2)	0.04±0.01	0.08±0.02	0.08±0.02
	Permanent environment effect (c^2_{pe})	0.01±0.01	0.06±0.02	0.10±0.02
Services per Conception (SPC)	Additive genetic PSD	0.02072	0.02072	0.0221
	Additive genetic lower HPD	0.07458	0.07458	0.05537
	Additive genetic upper HPD	0.15580	0.15580	0.1420
	Additive genetic variance (σ_a^2)	0.11520	0.11520	0.09869
	Environmental variance (σ_e^2)	1.00000	1.00000	1.0000
	Permanent environmental variance (σ_{pe}^2)	0.03289	0.03289	0.1256
	Direct heritability (h^2)	0.10±0.02	0.07±0.01	0.06±0.01
	Permanent environment effect (c^2_{pe})	0.14±0.02	0.07±0.02	0.10±0.02

The highest posterior density (HPD) confidence interval for the categorical trait pregnant within 100d post-partum (PD100d) additive genetic variance ranged from a minimum of -0.03928 to a maximum of 0.18160 depending on the two-trait combination. Heritability estimates ranged from 0.07±0.01 to 0.08±0.02 for PD100d depending on the bivariate combination. Potgieter *et al.* (2006) reported an estimate of heritability of 0.05±0.02 for PD100d using a linear animal model, which is slightly lower in absolute magnitude.

The highest posterior density (HPD) confidence interval for the categorical trait pregnant within 200d post-partum (PD200d), additive genetic variance ranged from a minimum of -0.03928 to a maximum of 0.18160 depending on the bivariate combination. Heritability estimates ranged from 0.06±0.04 to 0.08±0.02 for PD200d depending on the two-trait combination.

The highest posterior density (HPD) confidence interval for the linear trait days open (DO) additive genetic variance ranged from a minimum of -85.82 to a maximum of 748.00 depending on the two-trait combination. Heritability estimates ranged from 0.05±0.02 to 0.08±0.05 for DO depending on the bivariate combination. Potgieter *et al*. (2006) derived a heritability estimate for DO of 0.04±0.02 in South African Jerseys using a linear animal model. Dematawewa & Berger (1998) also reported a heritability estimate of 0.04 for DO in Holsteins using a linear animal model. Restricting DO to be between 50 and 250 days, Van Raden *et al*. (2004) found a heritability of 0.037 for DO in US Holsteins. Oseni *et al*. (2004) derived heritability estimates for DO of between 0.03 and 0.06 in US Holsteins with different editing criteria, and concluded that DO was strongly influenced by management protocols.

The highest posterior density (HPD) confidence interval for the linear trait calving to first service (CFS) additive genetic variance ranged from a minimum of 42.23 to a maximum of 85.96 depending on the two-trait combination. Heritability estimates ranged from 0.08±0.02 to 0.09±0.03 for CFS depending on the bivariate combination. Potgieter *et al.* (2006) reported a heritability for CFS of 0.01±0.02 using a linear animal model in a study conducted on reproduction parameters for South African Jerseys. Wall *et al*. (2003) reported a heritability of 0.04 for days from calving to first service. The heritability estimates for CFS were thus slightly higher than those from previous studies, although agreeing with the estimate of Jamrozik *et al*. (2005).

The highest posterior density (HPD) confidence interval for the linear trait services per conception (SPC) additive genetic variance ranged from a minimum of 0.08737 to a maximum of 0.32100, depending on the two-trait combination. Heritability estimates ranged from 0.05±0.02 to 0.07±0.02 for CFS depending on the bivariate combination. Wall *et al*. (2003) reported a heritability of 0.02 for number of inseminations per conception. González-Recio *et al*. (2005) found that heritability of SPC ranged between 0.038 and 0.050 using ordinal censored threshold and sequential threshold models, which is in fair agreement with the present results. In a study conducted by Potgieter *et al.* (2006), a heritability of 0.04±0.02 for SPC was derived using a linear animal model. Weller & Ezra (2004) studied female fertility as the inverse of the number of inseminations to conception in Israeli Holstein dairy cattle using a linear animal model, and found heritability estimates ranging between 0.02 and 0.03. Veerkamp *et al*. (2001) reported a heritability estimate of 0.03 for SPC using a linear model. Fitting a negative binomial model, Tempelman & Gianola (1999) estimated a heritability of 0.02 for SPC. The estimates derived in this study are slightly higher than most previously published values, although, in general, studies using threshold models tend to give a slightly larger heritability for SPC.

Judging from the heritability estimates and computing time, interval traits seem to be effective for genetic improvement of reproductive traits. This study included some records in which calving date of next parity is reported, but pregnancy diagnosis and calving date of next parity are unnecessary for calculating a trait like CFS. Depending on data availability and appropriate data editing criteria, CFS might be more suitable for genetic evaluation than DO.

Table 4.3 reports genetic, permanent environmental and residual correlations among fertility traits in South African Holsteins using linear-linear and linear-threshold analyses. Direct genetic correlations between the reproductive traits ranged from 0.99 between DO and PD100d to -0.98 between DO and PD200d. Days open also had favourable relationships with FS80d and PD200d indicating that increasing DO would have resulted in fewer cows inseminated within the first 80 days post-partum and also fewer cows confirmed pregnant within 200 days post calving.

Table 4.3 Genetic, permanent environmental and residual correlations between fertility traits in South African Holsteins using linear–linear and linear-threshold analyses

Linear Traits	Type of Correlation	FS80d	PD100d	PD200d
Days Open (DO)	Genetic	-0.50±0.01	0.99±0.01	-0.98±0.02
	Permanent Environmental	-0.34±0.02	0.99±0.01	-1.00±0.01
	Residual	-0.25±0.01	0.97±0.01	-0.99±0.01
Calving to First Service (CFS)	Genetic	0.03±0.01	0.64±0.01	-0.36±0.01
	Permanent Environmental	0.12±0.01	0.42±0.03	-0.19±0.02
	Residual	0.04±0.01	0.49±0.01	-0.15±0.01
Services per Conception (SPC)	Genetic	0.01±0.14	-0.88±0.16	-0.90±0.15
	Permanent Environmental	0.14±0.18	-0.93±0.18	-0.93±0.16
	Residual	0.09±0.01	-0.91±0.01	-0.77±0.01

CFS had a positive genetic correlation with PD100d (0.64±0.01) suggesting that increasing the average number of days to first service would increase the number of cows confirmed pregnant by 100 days post-partum; although, reducing the number of cows confirmed pregnant by 200 days post-partum. The favourable genetic relationship between SPC and PD100d (-0.88±0.16) and between

SPC and PD200d (-0.90±0.15), demonstrated that increasing the number of services, fewer cows will be confirmed pregnant by 100 and 200 days post-partum. This implies that cows needing more inseminations to get pregnant, will take longer to be confirmed in calf.

Relatively small posterior standard deviations were associated with these estimates, indicating their relatively high precision, with the exception of the PE correlation between FS80d and and SPC (0.14±0.18). Results indicated positive associations between common environments in later lactations for DO and PD100d, CFS and PD100d. These results indicate that fewer DO and fewer days for CFS can result in higher pregnancy rates at PD100d. Negative relationships were observed for SPC and PD100d, SPC and PD200d, which meant that more SPC was associated with lower pregnancy rates at PD100d and PD200d. The level of management in herds may partially be the reason for these relationships. In herds with a lower level of management the reproductive performance of cows will also be lower.

Table 4.4 Genetic correlations (above diagonal) and residual correlations (below diagonal) between binary and linear traits indicative of fertility in South African Holsteins

Traits	**Traits**	**FS80d**	**PD100d**	**PD200d**
Binary traits	FS80d	-	0.54±0.16	0.60±0.15
	PD100d	0.42±0.17	-	0.95±0.20
	PD200d	0.12±0.02	0.97±0.02	-
	Traits	**DO**	**CFS**	**SPC**
Linear traits	DO	-	0.56±0.11	0.03±0.01
	CFS	0.28±0.01	-	0.99±0.19
	SPC	0.04±0.01	0.81±0.02	-

In general, high genetic correlation estimates were obtained among the different fertility traits. CFS showed medium to large estimated correlations with most of the fertility traits, but close to zero with FS80d. This indicates that a strong genetic relationship exist between a cow's ability to recover its normal reproduction function after calving and the ability to conceive after exhibiting heat**.**

Genetic parameters for female reproductive traits have been a subject of numerous publications in recent years (Jansen, 1986; Jansen *et al*., 1987; Weller, 1989; Raheja *et al*., 1989; Hayes *et al*., 1992; Weigel & Rekaya, 2000; Kadarmideen *et al*., 2003; Andersen-Ranberg *et al*., 2003; Muir *et al*., 2004). Several studies indicated unfavourable genetic correlation between fertility and production traits in dairy cattle (Kadarmideen *et al*., 2003; Wall *et al*., 2003). Correct modeling of fertility traits would require inclusion of production data in the model as correlated traits.

4.4 Conclusion

Variance ratio estimates obtained in the current study were consistent with results from other studies. Heritabilities of most reproductive traits were generally below 0.10, as reported in literature cited. Genetic correlations between different fertility parameters analyzed in our study indicated that it is unlikely that a single characteristic would serve well for selection purposes. Different traits can be combined in a fertility index that could be used for selecting for an improved fertility, defined as the successful birth of a calf following a successful timely conception and gestation period. Reducing the number of traits in the fertility index to 4 or 5 would facilitate better understanding of the index by breeders. Heifer traits are measured relatively early in the cow's life and therefore they should be included in any fertility index. Further research in constructing an optimal fertility index is warranted.

CHAPTER 5

THE EFFECT OF PRODUCTION TRAITS ON FERTILITY IN SOUTH AFRICAN HOLSTEIN COWS

5.1 Abstract

Genetic parameters for South African Holstein cows for fertility and production traits were estimated from 2414 lactation records. A series of bivariate analyses were done on a combination of fertility and production traits using linear-linear and linear–binary analysis. The software used was THRGIBBS1F90. Fertility traits were days from calving to first service (CFS), days from calving to conception (DO), percentage cows inseminated within 80d post-partum (FS80d), number of services per conception (SPC), and the binary traits percentage of cows pregnant within 100d and 200d post-partum (PD100d, Pd200d). Milk production traits were 300-day milk, fat and protein yield. For fertility traits, the range of heritability (h^2) estimates was 0.006 to 0.08 for linear traits and 0.05 to 0.12 for binary traits. Genetic correlations of fertility with milk production traits were generally unfavourable (range −0.93 to 0.76)

5.2 Introduction

The economic importance of fertility traits in dairy cattle is well established (Esslemont, 1982; Holmann *et al*., 1984; Dijkhuizen *et al*., 1985). Dairy cow fertility is important both economically and ethically. Good fertility in cows is important for keeping the calving interval within acceptable limits, reducing the number of inseminations and reducing culling due to reproductive failure. High milk yield and certain conformation traits have been the primary selection objectives in dairy farming for a number of decades. Many secondary traits, such as reproduction traits and health traits, however, are important in minimizing cost and maximizing the net return of the dairy enterprise. Controversy has long existed whether or if so, to what extent reproductive performance is affected by milk yield. Gaines (1927) noted that lactation affected reproductive function and that a prevalent opinion of dairy producers was that managing cows "to secure as high a level of milk production as possible has a tendency to interfere with the occurrence of conception". Data collected prior to 1970 have shown little or no association between milk yield and reproduction (Boyd *et al*., 1954; Currie, 1956). However, adverse effects of milk yield on reproductive performance have been reported by many investigators since.

Many studies have shown negative genetic relationships between fertility traits and milk yield. Some researchers contended that is selection is for milk production only, it would lead to a genetic decline in cow fertility (Hoekstra *et al*., 1994; Pryce *et al.,* 1997; Dematawewa & Berger, 1998; Kadarmideen *et* *al.,* 2000). Thus, incorporation of fertility in selection decisions seems desirable. Currently, only few countries have national selection indices that include fertility traits. To support future profitability in production systems that penalise poor fertility, routine national sire or cow genetic evaluations for fertility must be derived and incorporated in a multi-trait national genetic index. This will enable dairy farmers to select the best animals based on a combination of production and fertility.

Estimates of the relationship between (milk?) production and fertility from field data may be difficult to interpret owing to confounding management decisions with biological effects (Philipsson, 1981; Jansen, 1985). The inherent problem in fertility analysis is that certain traits may have been subjected to censoring and selection based on milk yield. For example, cows that are culled for low milk production would have no calving interval records regardless of their reproductive efficiency. Dairy producers may give more opportunities to high producing cows to conceive and may deliberately delay inseminations after calving for these cows. High producing cows may have fertility problems resulting in a longer days to first insemination and calving interval. It may not be possible to differentiate between cows experiencing fertility problems and cows of which the first insemination was deliberately delayed because of a management decision. Milk yield can be included as a covariate in the analysis of fertility but that can only correct reproductive measures with respect to phenotypic differences in milk yield. A multi-trait analysis of fertility traits, with production traits as additional traits is a different approach which aims to improve the accuracy of genetic evaluations for the traits involved by reducing variances of prediction error of estimated breeding values (Schaeffer, 1984) and providing breeding values for animals that are not recorded for a particular trait.

Animals may have been highly selected for milk yield in early lactation, which can lead to biased fertility observations in the current or later lactation in the form of presence or absence of subsequent calving, and timing and frequency of inseminations. The preferential treatments of cows are also practised at genetic level such as favouring daughters of elite sires reknown for the high genetic merit for milk production by daughters'. Single-trait analysis, ignoring information on selective treatment of cows with different (genetic potential for) milk yield, would lead to biased genetic parameters, which in turn, would result in inappropriate predictions based on multi-trait national selection indexes.

Furthermore, some caution should be exercised when using interval measures as fertility traits. Calving to first service (CFS), for instance, has an unfavourable correlation with milk production. However this relationship could be forced by non-genetic effects such as later inseminations and a larger number of chances given to higher producers to get pregnant (Thaller, 1997).

Although the genetic correlation between fertility and milk production traits is generally antagonistic, these associations are also influenced by level of production and management (Haile-Maraim *et al.*, 2003). Cows are producing at their maximum level when they are expected to show signs of oestrus and conceive. In early lactation, cows are also in negative energy balance and will mobilize body reserves to meet the increase nutrient demands for milk production. At the same total milk output, cows with a lower peak milk production and greater persistency may experience less energy imbalance (and thus less reproductive failure) than cows with a higher peak production. Pryce & Veerkamp (2001) reviewed recent literature and reported that the genetic correlation between calving interval and milk production ranged from 0.22 – 0.59. Several researchers have also reported that the genetic antagonism between fertility and milk production increased with parity (Dermatawewa & Berger, 1998; Roxström *et al*., 2001; Haile-Maraim *et al*., 2003). Haile-Maraim *et al.* (2003) reported high across parity genetic correlations between milk production and calving interval, suggesting that high milk production in first lactation could result in poor reproduction performance in subsequent lactations.

5.3 Materials and Methods

5.3.1 Data

DIMMSA is dairy herd management software programme used in South Africa by some dairy producers. The outcome of each AI event was thus known in a number of herds. These insemination records were linked to the calving date of each cow, lactation number, dam and sire identification numbers. By using this information, fertility traits that measure the ability of a cow to show heat early in the breeding period and the probability of success of insemination and confirmation of pregnancy were derived. These fertility traits were defined based on data availability in a way that they would describe a complete picture of the reproductive history for the cows. Before analyses, records with missing sire and dam identification numbers were removed from the data set. The data set from DIMMSA was merged with a production data set, including milk production, fat and protein yield.

5.3.2 Data editing

Data on insemination and calving events of 14 South African Holstein herds, from 1991 to 2007, were obtained from DIMMSA. All cows were required to have some form of valid identification number. The data set included cows that had no subsequent calving date. These records were retained in the data set, as excluding them would lead to biased data set (i.e., data with only fertile and/or high yielding cows. Records up to the first six lactations were retained for the analysis. The final data set consisted of 2414 lactation records from 812 cows in 3 herds. The characteristics of this data set are given in Table 5.2.

5.3.3 Statistical analysis

The data was analysed using bivariate linear-linear and linear-threshold animal models. The fixed effects fitted were herd (3 levels), year (17 levels), season (4 levels) and lactation number (6 levels). The traits analysed were interval from calving to first service (CFS), interval from calving to conception (DO), number of services per conception (SPC), (all linear) and as binary traits (coded 0=no and 1=yes) whether cows were inseminated for the first time within 80d post-partum (FS80d), whether cows were confirmed pregnant within 100d post-partum (PD100d) and whether cows were confirmed pregnant within 200d post-partum (PD200d).

The model included the random effects of animal and animal permanent environment (PE). The software used was THRGIBBS1F90 (Misztal, 2008). Single chains of 250 000 cycles were run, with the first 50 000 cycles used as the burn-in period. This was followed by post Gibbs analysis, using POSTGIBBSF90 (Misztal *et al*., 2002) to determine convergence by visual examination of plots of variance componemts plotted against iterations. Posterior means were used to calculate the heritability and animal PE variance ratios for each trait. Genetic, animal PE and residual correlations were calculated accordingly. The same multi-trait model as described in Chapter 4 was implemented.

5.4 Results and Discussion

In Table 5.2 it was evident that means and standard deviations (in parenthesis) of the interval from calving to first service (CFS) within lactations were 88(46), 82(47), 80(41), 76(40), 77(44) and 73(30) days for lactations 1–6, respectively, with an overall mean and standard deviation (S.D.) of 82(44) days. Within-lactation phenotypic mean and S.D.'s of most fertility traits from parity one to six showed that fertility traits of cows remained about the same for some traits (e.g. SPC, PD100d, PD200d) but tended to improve from early to late parities for traits such as CFS, DO and FS80d. Part of this improvement may be due to the fact that only cows with above average fertility survived to the sixth lactation while cows of lower average fertility, may have been culled earlier. The overall phenotypic mean and SD for all other fertility and production traits are also presented in Table 5.2. The overall average DO was 111 days with an average of 64% of cows being inseminated within 80d after calving, with (on average) 2 inseminations per conception, 25% of cows pregnant within 100d post-partum and 58% pregnant within 200d post-partum.

Table 5.2 Within parity and overall phenotypic means and standard deviations (in parenthesis) for fertility and production traits ([a]CFS, interval calving to first service; DO, interval from calving to conception; SPC, number of services to conception; FS80d, percentage of animals inseminated within 80d post-partum; PD100d, percentage of animals confirmed pregnant within 100d post-partum, PD200d, percentage of animals confirmed pregnant within 200d post-partum; Milk, 300d milk production; Fat, 300d fat production; Protein, 300d protein production; [b] Binary trait scored as 1 = yes and 0 = no)

Parity	**CFS[a] (days)**	**DO[a] (days)**	**SPC[a] (n)**	**FS80d [b]**	**PD100d[b]**	**PD200d[b]**	**Milk (kg)**	**Fat (kg)**	**Protein (kg)**
1	88	117	1.99	0.56	0.28	0.61	7078	272	229
	(46)	(88)	(1.9)	(0.50)	(0.66)	(0.69)	(1946)	(76)	(59)
2	82	112	1.98	0.64	0.23	0.57	7582	296	246
	(47)	(87)	(1.8)	(0.48)	(0.68)	(0.73)	(2094)	(79)	(62)
3	80	114	2.1	0.67	0.21	0.57	7923	306	254
	(41)	(87)	(1.9)	(0.47)	(0.67)	(0.73)	(2098)	(79)	(63)
4	76	103	1.95	0.70	0.32	0.60	7695	296	245
	(40)	(83)	(1.85)	(0.46)	(0.70)	(0.72)	(2081)	(78)	(62)
5	77	103	2.0	0.68	0.22	0.53	7769	297	247
	(44)	(86)	(1.9)	(0.47)	(0.72)	(0.77)	(2000)	(73)	(59)
6	73	100	2.0	0.71	0.22	0.52	7302	284	232
	(30)	(86)	(2.0)	(0.45)	(0.73)	(0.78)	(1811)	(65)	(56)
Overall	82	111	2.0	0.64	0.25	0.58	7509	290	241
	(44)	(87)	(1.89)	(0.48)	(0.69)	(0.72)	(2049)	(78)	(61)

According to Table 5.3,, the highest posterior density (HPD) confidence interval for milk yield additive genetic variance ranged from a minimum of 427.2 to a maximum of 4487 depending on the two-trait combination. Heritability estimates ranged from 0.12±0.05 to 0.13±0.05 for milk yield, depending on the bivariate trait combination. The differences in heritability estimates may be due to sire versus animal models, differences in the mean and standard deviations of the traits analysed, and the statistical methods used to estimate parameters. A further possible reason for the difference in heritabilities is that in this study, heritabality estimates were estimated across parity and not within parity like many previous studies.

The highest posterior density (HPD) confidence interval for fat yield additive genetic variance ranged from a minimum of 105 to a maximum of 697.70 depending on the two-trait combination. Heritability estimates ranged from 011±0.03 to 0.14±0.04 for fat yield depending on the bivariate trait combination.

Table 5.3 Mean (co)variance components, posterior standard density (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios for some fertility traits and production traits in South African Holstein cows using a bivariate linear–linear and linear – threshold analyses

		Yield traits (kg)		
Trait	**Item**	**Milk**	**Fat**	**Protein**
Days Open (DO)	Additive Genetic PSD	100.3	141.20	76.47
	Additive genetic lower HPD	427.2	116.40	52.57
	Additive genetic upper HPD	4359	670.3	352.30
	Additive genetic variance (σ_a^2)	2393	393.10	202.40
	Environmental variance (σ_e^2)	12490	2035	1240
	Permanent environmental variance (σ_{pe}^2)	5056	505.7	424.30
	Direct heritability (h^2)	0.12±0.05	0.14±0.04	0.11±0.04
	Permanent environment effect (c^2_{pe})	0.25±0.05	0.18±0.05	0.22±0.04
Calving to First Service (CFS)	Additive genetic PSD	978.7	140.7	75.70
	Additive genetic lower HPD	549.5	114.60	65.22
	Additive genetic upper HPD	4386	666.20	362.00
	Additive genetic variance (σ_a^2)	5495	390.40	213.60
	Environmental variance (σ_e^2)	12520	2027	1233
	Permanent environmental variance (σ_{pe}^2)	4946	500.60	428.50
	Direct heritability (h^2)	0.12±0.05	0.13±0.04	0.11±0.04
	Permanent environment effect (c^2_{pe})	0.25±0.05	0.17±0.05	0.22±0.04
Services per Conception (SPC)	Additive genetic PSD	971.70	144.60	84.42
	Additive genetic lower HPD	655.40	130.70	50.21
	Additive genetic upper HPD	4464	697.70	381.10
	Additive genetic variance (σ_a^2)	2560	414.20	215.70
	Environmental variance (σ_e^2)	12490	2018	1247
	Permanent environmental variance (σ_{pe}^2)	4915	495.40	425.60
	Direct heritability (h^2)	0.13±0.05	0.14±0.05	0.11±0.05
	Permanent environment effect (c^2_{pe})	0.24±0.05	0.17±0.05	0.23±0.05
FS80d	Additive genetic PSD	896.9	137.50	80.89
	Additive genetic lower HPD	654.10	110	63.12
	Additive genetic upper HPD	4170	650.20	380.2
	Additive genetic variance (σ_a^2)	2412	380.60	221.70
	Environmental variance (σ_e^2)	12480	2021	1249
	Permanent environmental variance (σ_{pe}^2)	5028	514.70	416.80
	Direct heritability (h^2)	0.12±0.05	0.13±0.04	0.12±0.04
	Permanent environment effect (c^2_{pe})	0.25±0.05	0.18±0.04	0.22±0.05

Table 5.4 Mean (co)variance components, posterior standard density (PSD), 95% highest posterior density (HPD) confidence intervals and variance ratios for binary fertility and production traits in South African Holstein cows using a bivariate linear–threshold analyses.

Trait	Item	Milk	Fat	Prot
PD100d	Additive genetic PSD	956.80	135.60	74.09
	Additive genetic lower HPD	736	105	58.54
	Additive genetic upper HPD	4487	641.2	349.00
	Additive genetic variance (σ_a^2)	2611	360.3	203.80
	Environmental variance (σ_e^2)	12470	2005	1243
	Permanent environmental variance (σ_{pe}^2)	4883	520.1	420.7
	Direct heritability (h^2)	0.13±0.05	0.12±0.04	0.11±0.04
	Permanent environment effect (c^2_{pe})	0.24±0.05	0.19±0.05	0.23±0.04
PD200d	Additive genetic PSD	910	135.6	74.09
	Additive genetic lower HPD	639.2	105	58.54
	Additive genetic upper HPD	4207	641.2	349.00
	Additive genetic variance (σ_a^2)	2423	360.3	203.80
	Environmental variance (σ_e^2)	1249	2005	1243
	Permanent environmental variance (σ_{pe}^2)	5013	520.1	420
	Direct heritability (h^2)	0.12±0.05	0.11±0.03	0.10±0.03
	Permanent environment effect (c^2_{pe})	0.25±0.05	0.18±0.05	0.22±0.04

The highest posterior density (HPD) confidence intervals for the additive genetic variance ranged from a minimum of 52.57 to a maximum of 381.10 for protein yield depending on the two-trait combination. Heritability estimates ranged from 0.10±0.03 to 0.12±0.04 for protein yield.

Table 5.5 Genetic, permanent environmental and residual correlations between production and fertility traits in South African Holsteins using linear–linear and linear–threshold analyses

Linear Traits	Type of Correlation	Milk	Fat	Protein
Days Open (DO)	Genetic	0.20±0.15	0.04±0.01	0.02±0.02
	Permanent Environmental	0.23±0.01	0.10±0.03	0.40±0.004
	Residual	0.12±0.01	0.03±0.02	0.03±0.004
Calving to First Service (CFS)	Genetic	0.10±0.19	-0.01±0.22	0.76±0.17
	Permanent Environmental	0.38±0.02	-0.09±0.02	0.58±0.03
	Residual	-0.05±0.01	0.58±0.03	0.41±0.03
Services per Conception (SPC)	Genetic	-0.07±0.05	-0.07±0.1	-0.90±0.15
	Permanent Environmental	0.07±0.008	-0.01±0.002	-0.93±0.16
	Residual	0.20±0.008	0.23±0.006	-0.77±0.01
First service 80d (FS80d)	Genetic	0.40±0.01	0.35±0.002	0.23±0.003
	Permanent Environmental	-0.67±0.002	-0.74±0.00	-0.71±0.000
	Residual	-0.001±0.002	0.03±0.00	0.005±0.000
PD100d	Genetic	0.44±0.04	0.27±0.01	-0.36±0.02
	Permanent Environmental	-0.44±0.007	0.63±0.00	-0.10±0.002
	Residual	-0.29±0.00	-0.44±0.00	-0.07±0.002
PD200d	Genetic	-0.14±0.06	-0.007±0.02	-0.36±0.02
	Permanent Environmental	-0.28±0.00	0.01±0.001	-0.10±0.00
	Residual	-0.05±0.00	0.01±0.001	-0.07±0.00

Genetic, residual and permanent environmental correlations between fertility and production traits are presented in Table 5.5. The estimated genetic correlations between the interval reproduction traits and the yield traits ranged from -0.07 to 0.40 for milk yield, -0.07 to 0.35 for fat yield and -0.92 to 0.76 for protein yield. The genetic correlations between binary fertility traits and production traits varied from -0.36 to 0.44 The results obtained in this study are similar to previous studies, with the exception of the binary traits. In previous studies the genetic correlations between binary fertility traits and production traits were estimated to be between −0.17 to −0.35 (Dematawewa & Berger, 1998; Haile-Mariam *et al.,* 2003; Kadarmideen *et al.,* 2003).

Judging from the heritabilities, genetic correlations and data availability, reproductive traits in cows seem to be suitable for selection purposes, but these relationships suggest that intense selection for such traits would result in the deterioration of production traits. This is unacceptable for farmers, so such a strategy would not be favoured at present. Therefore, to improve reproductive performance, it is necessary to bring about changes in attitudes of the farmers, by stressing the economic and welfare benefits. The optimum balance of better reproduction and milk production should be examined.

5.5 Conclusion

Analysis of fertility traits is known to be problematic as fertility observations are subject to managerial decisions and observing some fertility traits depend on observing some other fertility traits. For example, cows that do not conceive, do not have records for number of inseminations per conception, days open or a subsequent calving date (hence no calving interval value), although having records that indicate the time of first insemination and whether this insemination ocured within 80 days post calving. The reason for cows not conceiving (and therefore no calving interval) could be due to biological reasons (inability to conceive) or because she was culled due to a poor milk yield (managemental decision). Elimination of cows from the data sets that do not conceive or calve down again would lead to biased results as data sets may contain either only fertile cows or high milk yielders or both. In our study, these biases were excluded because the data-editing procedure included all cows (with or without subsequent calving date). Among cows that do not conceive readily, farmers may re-inseminate those with superior milk yield or which are daughters of elite sires (Weller, 1989). This means that there could be preferential treatment with respect to genetic merit for milk yield. Bivariate analysis of fertility with milk yield studied here is recommended as an approach to account for such preferential selection of cows based on their (genetic merit for) milk yield.

In future, culling/selection effects of milk yield on fertility evaluations could be further investigated by estimating breeding values from bivariate analyses of test-day milk yields with lactation-based fertility measurements, as cows may vary in their fertility status depending on the stage of lactation. For example, cows may conceive easier in the early than the later part of lactation. In view of economic importance of cow fertility and the existence of genetic variation for many fertility traits, as shown here, routine national genetic evaluation and selection for female fertility are recommended.

CHAPTER 6

GENERAL CONCLUSIONS AND RECOMMENDATIONS

Dairy farmers do not have any control over the cost of inputs or the price of milk. They are therefore under pressure to increase the productivity of their dairy herds to ensure financial sustainability. This has resulted in farmers continuously selecting higher producing cows, as high milk yields are generally positively related to net farm profit. Recently, it has been noted that this process has resulted in a reduction in the sustainability of dairy production systems as farmers are finding it increasingly more difficult to get cows to conceive within a reasonable period after calving or to get them to conceive at all. Various reasons could contribute to this, i.e. larger dairy herds with less emphasis on individual animals, higher milk yields, a reduction in concentrate feeding, labourers increasingly unfamiliar with the physiology of reproduction. It has also been suggested that genetic changes as pertaining to the fertility merit of cows have occurred over time. In some countries. The so-called Holsteinization of dairy herds has been blamed for the reduction the fertility of dairy cows. The fertility of dairy cows affects their ability to calve down, i.e. to start a new lactation to ensure a high milk yield during the early part of the lactation and to ensure genetic improvement in the dairy herd. Moreover, farming systems also need to be sustainable in terms of the environment and animal welfare. There is at present a considerable interest in finding new ways of reducing costs and increasing efficiency at farm level.

Until recently, milk production, including fat and protein yield, has been the main objective for selection in most countries. Although milk production is clearly a major component of profitability, the emphasis it has received is also due to the ease of measurement compared to some other components of profitability. However, continued selection for higher milk production has been questioned on a number of grounds as it has been widely associated with deleterious effects on health, fertility and welfare of cows. As such, annual total culling rates should not be higher than 18% to maximise the benefit of age and genetic improvement. The effect of longer calving intervals is manifested in terms of lower annual milk yield, fewer calves sold per year, increased costs through a longer dry period and reduced profit associated with a calving down date move from a more profitable month of calving to one less profitable especially for seasonal and pasture based production systems. Other increased costs associated with increased calving interval are more inseminations per conception and extra veterinary treatments.

To improve the reproductive performance of dairy cows through genetic means, some way should be found to derive meaningful breeding values to discern cows with a high genetic merit for fertility from those with a low genetic merit. Calving interval (CI) is currently being used as an indicator of fertility for Holstein cows in South Africa. The problem with this trait is that it depends on subsequent calving dates, while there are no CI records for heifers and cows not calving again. Farmers usually cull cows that do not become pregnant at all or within a set time frame. This results in managers maintaining acceptable standards while not addressing the problem of poor reproduction management. A simple way to determine the standard of reproduction would be to determine the percentage of cows confirmed pregnant of all cows which are supposed to be pregnant, i.e. all cows more than 100 and 200 days in milk. By culling cows not becoming pregnant, the reproductive information of such cows is ignored in the genetic analysis of cows and bulls, possibly resulting in an overestimation of their genetic merit for fertility. Calving interval is the result of a number of events (traits) which could be used separately or in combination as fertility indicators.

In this study, alternative traits to CI were defined and genetic parameters of these traits, estimated. These traits included the following: the interval between calving and first service (CFS), the interval from calving to conception (DO), number of services per conception and whether CFS was within 80 days after calving and whether cows were confirmed pregnant by either 100 or 200 days after calving. Using these traits, the standard of reproduction management could be determined for individual farmers and compared specifically to Australian norms, where a similar, although larger, study was conducted. This study therefore provides an initial analysis of the standard of reproduction management in South African Holstein herds. Generally the standard of reproduction management in these dairy herds is not very high. It seems that farmers have adopted reproduction management systems in a desperate attempt to overcome poor reproduction. All these reproduction traits were significantly affected by herd, calving year, calving season and lactation number of which herd (managers) had the largest effect in magnitude. Interval traits showed an increase over time, although it reached a plateau of 80 days for the interval CFS and 140 days for DO, probably indicating a large management effect on these interval traits.

In the second part of this study, genetic parameters were estimated for these traits providing an indication of the expected response to selection in dairy herds. The same data source was used for the estimation of genetic parameters. Data were analysed using bivariate linear-linear and linear-threshold animal models with fixed effects being herd, year and season of calving and lactation number. Heritability estimates ranged from 0.04±0.01 to 0.10±0.02 for FS80d, from 0.07±0.01 to 0.08±0.02 for PD100d and from 0.06±0.04 to 0.08±0.02 for PD200d depending on the two-trait combination. Although heritability estimates of most fertility traits were below 0.10, they were consitent with those published by other researchers using linear models. Genetic correlations between different fertility parameters analyzed in this study indicated that it is unlikely that there is a single characteristic that would serve well for selection purposes; however, combining different traits could be considered in selection programmes to improve fertility.

Because fertility in dairy cows is either poorly, or not at all, accounted for in most dairy cattle breeding programs, little response has been observed over time. Although heritability estimates for most fertility traits analyzed were low, genetic change involves a cumulative effect over time. It must be accepted that management has a large effect on the reproductive performance of dairy cows. Poor reproduction management could reduce the impact of genetic change, while veterinary interventions or better reproduction management (or good managers) could improve the reproductive performance of cows of low genetic merit for fertility. This emphasizes the fact that the whole process of reproduction is rather complex with numerous factors which have to be combined to enable cows to perform well.

The industry should be encouraged to provide reproductive records of cows to enable the estimating of genetic parameters and to derive estimated breeding values (EBV) for fertility for cows and bulls with substantial numbers of daughters. As no single trait analyzed in this study shows a high correlation with all traits, it seems that a combination of traits should be used as an indicator of fertility. Further research in constructing an optimal fertility index is warranted.

A national fertility index, expressed as economic weightings that describe the economic impact of a unit trait change, should stipulate the fertility characteristics to be improved and the desired direction for genetic change. The national fertility index should take into account parameters such as heritability and genetic correlations between fertility traits and milk production traits and be part of the National Performance Testing Scheme.

The principles and methods for the definition of a national genetic fertility index, derivation of economic values and fertility index construction have been well established in several international studies. It will be necessary to re-calculate parameters and re-derive economic values, at least every generation (± 5 years), to ensure that the breeding objective and fertility index is optimal. Furthermore, a long term commitment to systematic recording of economic important fertility traits at producer level is of utmost importance in the development of a national fertility index.

It seems obvious, from these final remarks that the three key elements for sustainable genetic improvement in fertility can be summarized as follows. The first element is definition of a national fertility index which defines the value of genetic change in a range of fertility traits and establishes the direction to breed, in economic terms. Application of these results is necessary if the South African Holstein industry is to maximise the exploitation of genetics and to improve profitability and longivety in the breed.

Using information to identify and select animals with superior genetic merit for fertility is the second key element. This obviously necessitates an evaluation system which provides the estimates of genetic merit for each animal for all the identified economically important fertility traits. Where important fertility traits are not included in the National Performance Testing Scheme, the necessary steps should be taken for these traits to be included. If a lack of parameter information exists should be rectified with research directed at these traits and criteria. Breeders should also be informed of these new developments and should be educated to adapt technological and management practices that will enable them to measure these fertility traits.

References

Allaire, F.R. & Cunningham, E.P., 1980. Culling on low milk yield and its economic consequences for the dairy herd. *Livestock Production Science*, 7: 349-359.

Andersen-Ranberg, I.M., Klemetsdal, G., Heringstad, B., Svendsen, M. & Steine, T., 2002. Breeding values for daughter fertility in Norwegian dairy cattle; data quality and model validation. *INTERBULL Bulletin,* 29: 200-204.

Andersen-Ranberg I.M., Heringstad, B., Klemetsdal, G., Svendsen, M. & Steine, T., 2003. Heifer fertility in Norwegian dairy cattle: Variance components and genetic change. *Journal of Dairy Science*, 86(8): 2706-2714.

Andersen-Ranberg I.M., Klemetsdal, G., Heringstad, B. & Steine, T., 2005. Heritabilities, genetic correlations, and genetic change for female fertility and protein yield in Norwegian dairy cattle. *Journal of Dairy Science,* 88(1): 348-55.

Arbel, R., Bigun, Y., Ezra, E., Sturman, H. & Hojman, D., 2001. The effect of extended calving intervals in high-yielding lactating cows on milk production and profitability. *Journal of Dairy Science,* 84(3): 600-608.

Averill, T.A., Reykaya, R. & Weigel, K., 2004. Genetic analysis of male and female fertility using longitudinal binary data. *Journal of Dairy Science,* 87: 3947-3952.

Bailie, J.H., 1982. Management and economic effects of different levels of oestrus detection in the dairy herd. *The Veterinary Record*, 110(10): 218-221.

Ball, P.J.H. & Peters, A.R., 2004. Reproduction in cattle. Third Edition. Blackwell Publishing Ltd. 9600 Garsinton Rd. Oxford OX4 2DQ, UK.

Barnes, M., 2001. Reproduction and Lactation. Principles and Practices in Bovine Reproduction: Blacksburg. Virginia, USA.

Beam, S.W. & Butler, W.R., 1999. Effects of energy balance on follicular development and first ovulation in post-partum dairy cows. *Journal of Reproduction and Fertility Supplement*, 54:411-424.

Beever, J.E., Smit, M.A., Meyers, S.N., Hadfield, T.S., Bottema, C., Albretsen, J. & Cockett, N.E., 2006. A single-base change in the tyrosine kinase II domain of ovine *FGFR3* causes hereditary chondrodysplasia in sheep. *Animal Genetics*, 37: 66-71.

Best, N.G., Cowles, M.K. & Vines, S.K., 1995. *CODA Manual version 0.30*. MRC Biostatistics Unit, Cambridge, UK. 41pp.

Biffani, S., Marusi, M., Biscarini, F. & Cavanesi, F., 2005. Developing a genetic evaluation for fertility using angularity and milk yield as correlated traits. *Interbull Bulletin*, 33: 63-66.

Boichard, D. & Manfredi, E., 1994. Genetic analysis of conception rate in French Holstein cows. *Acta Agriculturae Scandinavica*, 44: 138-145.

Boyd, L.J., Seath, D.M. & Olds, D. 1954. Relationship between level of milk production and breeding efficiency in dairy cattle. *Journal of Dairy Science*, 62: 1140-1144.

Braun, R.K., 1986. Analysis of reproductive records using DHIA summaries and other monitors in large dairy herds, in Morrow, D.A. (Editor). *Current therapy in Theriogenology*, 2nd edition. WB Saunders, Philadelphia. 414-418.

Britt, J.H., 1985. Enhanced reproduction and its economic implications. *Journal of Dairy Science*, 68(6):1585-1592.

Brotherstone, S., Banos, G. & Coffey, M.P., 2002. Evaluation of yield traits for the development of a UK fertility index for dairy cattle. *7th World Congress on Genetics Applied to Livestock Production.* 01-28.

Butler, W.R. &. Smith, R.D., 1989. Interrelationships between energy balance and post-partum reproductive function in dairy cattle. *Journal of Dairy Science*, 72(3):767-783.

Castillo-Juarez, H., Oltenacu, P.A., Blake, R.W., McCulloch, C.E. & Cienfuegos-Rivas, E.G., 2000. Effect of herd environment on the genetic and phenotypic relationships among milk yield, conception rate, and somatic cell score in Holstein cattle. *Journal of Dairy Science*, 83(4): 807-814.

Clay, J.S., & McDaniel, B.T., 2001. Computing mating bull fertility from DHI nonreturn data. *Journal of Dairy Science*, 84(5):1238-1245.

Currie, E.J., 1956. The influence of milk yield on fertility in dairy cattle. *Journal of Dairy Research*, 23: 301-308.

Darwash, A.O., Lamming, G.E. & Woolliams, J.A., 1997. Estimation of genetic variation in the interval from calving to post-partum ovulation of dairy cows. *Journal of Dairy Science*, 80(6):1227-1234.

Darwash, A.O., Lamming, G.E. & Woolliams, J.A., 1999. The potential for identifying heritable endocrine parameters associated with fertility in post-partum dairy cows. *Animal Science*, 68, 333-347.

De Vries, A., & Risco, C.A., 2005. Trends and seasonality of reproductive performance in Florida and Georgia dairy herds from 1976 to 2002. *Journal of Dairy Science*, 88(6):3155-3165.

Dematawewa, C.M.B. & Berger, P.J., 1998. Genetic and phenotypic parameters for 305-day yield, fertility, and survival in Hoisteins. *Journal of Dairy Science*, 81(10):2700-2709.

Dijkhuizen, A.A., Stelwagen, J. & Renkema, J.A., 1985. Economic aspects of reproductive failure in dairy cattle. Financial loss at farm level. *Preventive Veterinary Medicine*, 3: 251-263.

Eicker, S.W., Grohn, Y.T. & Hertl, J.A., 1996. The association between cumulative milk yield, days open, and days to first breeding in New York Holstein Cows. *Journal of Dairy Science*, 79(2): 235-241.

Erb, H.N., Martin, S.W, Ison, N. & Swaminathan, S., 1981. Interrelationships between production and reproductive diseases in Holstein cows. Conditional relationships between production and disease. *Journal of Dairy Science*, 64(2): 272-281.

Esslemont, R.J., 1982. Economic aspects related to cattle infertility and the post-partum interval. In: H. Karg and E. Schallenberger (Editors), Factors Influencing Fertility in the Post-partum Cow. Martinus Nijhoff Publishers, The Hague.

Esslemont, R.J., 1992. Measuring dairy herd fertility. *Veterinary Record,* 131: 209-212.

Esslemont, R.J. & Peeler, E.J., 1993. The scope for raising margins in dairy herds by improving fertility and health. *British Veterinary Journal*, 149: 537-547.

Ferguson, J.D., 1996. Diet, production and reproduction in dairy cows. *Animal Feed Science and Technology,* 59: 173-184.

Foulley, J.L., Gianola, D. & Im, D., 1987. Genetic evaluation of traits distributed as Poisson- binomial with reference to reproductive characters. *Theoretical and Applied Genetic*. 73: 870-877.

Fourichon, D., Seegers, H. & Malher, X., 2000 Effect of disease on reproduction in the dairy cow: a meta-analysis. *Theriogenology,* 53(9): 1729-1759

Freeman, E. A. 1984., Sire selection. Secondary traits: sire evaluation and the reproductive complex. *Journal of Dairy Science*, 67(2): 449-456.

Gaines, J.D., 1989a The role of record analysis in evaluating subfertile dairy herds. *Veterinary Medicine,* 84: 532-543.

Gaines, W.L., 1927. Milk yield in relation to recurrence of conception. *Journal of Dairy Science*, 10: 117-124.

Gianola, D., 1982. Theory and analysis of threshold characters. *Journal of Animal Science*, 54: 1079-1096.

González-Recio, O. & Alenda, R., 2005. Genetic parameters for female fertility traits and a fertility index in Spanish dairy cattle. *Journal of Dairy Science*, 88(9): 3282-3289.

González-Recio, O., Chang, Y.M., Gianola, D. & Weigel, K.A., 2005. Genetic analysis of number of inseminations to conception in Holstein cows using censored records and time-dependent covariates. *Journal of Dairy Science*, 88(10): 3655-3662.

González-Recio, O., Chang, Y.M., Gianola, D. & Weigel, K.A., 2006. Comparison of models using different censoring scenarios for days open in Spanish Holstein cow. *Animal Science*, 82: 233-239.

González-Recio, O., Pérez-Cabal, M.A. & Alenda, R., 2004. Economic value of female fertility and its relationship with profit in Spanish dairy cattle. *Journal of Dairy Science*, 87(9): 3053–3061.

Gröhn, Y., Erb, H..N., McCulloch, C.E. & Saloniemi, H.S., 1990. Epidemiology of reproductive disorders in dairy cattle : associations among host characteristics, disease and production. *Preventive Veterinary Medicine*, 8(1): 25-39.

Grosshans, T., Xu, Z.Z., Burton, L.J. & Johnson, D.L., 1996. Genetic parameters for fertility traits in seasonal dairy cattle. Dairy Cattle Breeding in New Zealand.

Grosshans, T., Xu, Z.Z., Burton, L.J., Johnson, D.L. & Macmillan, K.L., 1997. Performance and genetic parameters for fertility of seasonal dairy cows in New Zealand. *Livestock Production Science*, 51: 41-51.

Gutierrez, C.G., Gong, J.G., Bramley, T.A. & Webb, R., 2006. Selection on predicted breeding value for milk production delays ovulation independently of changes in follicular development, milk production and body weight. *Animal Reproduction Science*, 95:193-205.

Haile-Mariam, M., Bowman, P.J., & Goddard, M.E., 2003. Genetic and environmental relationships among calving interval, survival, persisitency of milk yield and somatic cell count in dairy cattle. *Livestock Production Science*, 80: 189-200.

Haile-Mariam, M., Bowman, P.J. & Goddard, M.E., 2004. Genetic and environmental relationship among calving interval, survival, persistency of milk yield and somatic cell count in dairy cattle. *Animal Science*, 80: 189-200.

Hansen, L.B., Freeman, A.E. & Berger, P.J., 1983. Variances, repeatabilities, and age adjustments of yield and fertility in dairy cattle. *Journal Dairy Science*, 66(2): 281-292.

Harris, B.L. & Kolver, E.S., 2001. Review of Holsteinization on intensive pastoral dairy farming in New Zealand. *Journal of Dairy Science*, 84(E. Suppl.): E56-E61.

Harrison, R.O., Ford, S.P., Young, J.W., Conely, A.J. & Freeman, A.E., 1990. Increased milk production versus reproductive and energy status in high-producing dairy cows. *Journal of Dairy Science*, 73(10): 2749-2758.

Hayes, J.F., Cue, R.I. & Monardes, H.G., 1992. Estimates of repeatability of reproductive measures in Canadian Holsteins. *Journal of Dairy Science*, 75(6):1701-1706.

Heersche, G.(Jr.), & Nebel, R.L., 1994. Measuring efficiency and accuracy of detection of estrus. *Journal of Dairy Science*, 77(9): 2754-2761.

Henry, E.T., 1986. Dairy herd reproductive efficiency, in Howard, J.L. (Editor). *Current veterinary therapy, food animal practice*, 2nd edition. Philadelphia: WB Saunders. 803-808

Herrnandez, J., Shearer, J.K. & Webb, D.B., 2001. Effect of lameness on the calving-to-conception interval in dairy cows. *Journal of the American Veterinary Medical Association*, 218(10): 1611-1614.

Heuwieser, W., Oltenacu, P.A., Lednor, A.J. & Foote, R.H., 1997. Evaluation of different protocols for prostaglandin synchronization to improve reproductive performance in dairy herds with low estrus detection efficiency. *Journal of Dairy Science*, 80(11): 2766-2774.

Hillers, J.K., Senger, P.L., Darlington, R.L. & Flemming, W.N., 1984. Effects of production, season age of cows, days dry, and days in milk on conception to first service in large commercial dairy hers. *Journal of Dairy Science*, 67(4): 861-867.

Hodel, F., Moll, J. & Kuenzi, N., 1995. Analysis of fertility in Swiss Simmental cattle – Genetic and environmental effects on female fertility. *Livestock Production Science*, 41(2): 95-103.

Hoekstra, J., Van der Lugt, A.W., Van der Werf, J.H.J. & Ouweltjes, W., 1994. Genetic and phenotypic parameters for milk production and fertility traits in upgraded dairy cattle. *Livestock Production Science*, 40(3): 225-232.

Hoeschele, I., 1991. Additive and non-additive genetic variance in female fertility of Holsteins. *Journal of Dairy Science*, 74(5):1743-1752.

Holmann, F.J., Shumway, C.R., Blake, R.W., Schwart, R.B. & Sudweeks, E.M., 1984. Economic value of days open for Holstein cows of alternative milk yields with varying calving intervals. *Journal of Dairy Science*, 67: 636-643.

Ireland, J.J., Mihm, M., Austin, E., Diskin, M.G. & Roche, J.F., 2000. Historical perspective of turnover of dominant follicles during the bovine estrous cycle: key concepts, studies, advancements, terms. *Journal Dairy Science,* 83(7): 1648-1658.

Jamrozik, J., Fatehi, J., Kistemaker, G.J. & Schaeffer, L.R., 2005. Estimates of genetic parameters for Canadian Holstein female reproduction traits. *Journal of Dairy Science*, 88(6): 2199-2208.

Jansen, J., 1985. Genetic aspects of fertility in dairy cattle based on analysis of A.I. of data - A review with emphasis on areas for further research. *Livestock Production Science*, 12: 1-12.

Jansen, J., 1986. Direct and maternal genetic parameters of fertility traits in Friesian cattle. *Livestock Production Science,* 15: 153-164.

Jansen, J., Van der Werf, J. & DeBoer, F.W., 1987. Genetic relationships between fertility traits for dairy cows in different parities. *Livestock Production Science*, 17: 337-349.

Kadarmideen, H.N., Thompson, R. & Simm, G., 2000. Linear and threshold model genetic parameter estimates for disease, fertility and production traits in UK dairy cattle. *Animal Science*, 71: 411-420.

Kadarmideen, H.N., Thompson, R., Coffey, M.P. & Kossaibati, M.A., 2003. Genetic parameters and evaluations from single- and multiple trait analysis of dairy cow fertility and milk production. *Livestock Production Science*, 81(2-3): 183-195.

Kearney, J.F., Schutz, M.M., Boettcher, P.J. & Weigel, K.A., 2004.Genotype environment interaction for grazing versus confinement. I. Production traits. *Journal of Dairy Science*, 87(2):501–9.

Lawes Agricultural Trust, 2007.

Lindhe, B. & Philipsson, J., 1998. Genetic correlations between production with disease resistance and fertility in dairy cattle and consequences for total merit selection. *Acta Agriculturae Scandinavica*, Section A 48(4): 216-221.

Lucy, M. C., 2001. Reproductive loss in high-producing dairy cattle: where will it end? *Journal of Dairy Science*, 84(6):1277-1293.

Mackey, D.R., Gordon, A.W., McCoy, M.A., Verner, M. & Mayne, C.S., 2007. Associations between genetic merit for milk production and animal parameters and the fertility performance of dairy cows. *Animal,* 1: 29-43.

Makgahlela, L., 2008. Calving interval now included in the national genetic evaluation. National Milk Recording and Improvement Scheme. Newsletter No 13. November 2008. p: 20.

Malvern, P.V., 1984. Pathophysiology of the puerperium: definition of the problem. Proceedings of the 10th International Congress of Animal Reproduction and Artificial Insemination.

Mandebvu, P., Uchida, K.C., Sniffen, C.J., Ballard, C.S., & Carter, M.P., 2000. Effect of feeding complexed zinc methionine, manganese methionine, copper lysine, and cobalt glucoheptonate on lactational and reproductive performances by lactating Holstein cows. *Journal of Dairy Science,* 83(Suppl 1): 303-304.

Markusfeld, O. & Ezra, E., 1993. Body measurements, metritis, and post-partum performance of first lactation cows. *Journal of Dairy Science* 76(12): 3771-3777.

Marti, C.F. & Funk, D.A., 1994. Relationship between production and days open at different levels of herd production. *Journal of Dairy Science*, 77(6): 1682-1690.

Mayne, C.S., McCoy, M.A., Lennox, S.D., Mackey, D.R., Verner, M., Catney, D.C., McCaughey, W.J., Wylie, A.R.G., Kennedy, B.W. & Gordon, F.J., 2002. Fertility of dairy cows in Northern Ireland. *Veterinary Record*, 150: 707-713.

Miglior, F., Muir, B.L. & Van Doormaal, B.J., 2005. Selection indices in Holstein cattle of various countries. *Journal of Dairy Science*, 88(3):1255-1263.

Miller, R.H., Clay, J.S. & Norman, H.D., 2001. Relationship of somatic cell score with fertility measures. *Journal of Dairy Science*, 84(11): 2543 – 2548.

Misztal, I. & Rekaya, R., 2004. Fertility and factors in days open. International Dairy Heat Stress Consortium Feb. 28-29, 2004, Florida. USA.

Moore, R.K., Kennedy, B.W., Schaeffer, L.R. & Moxley, J.E., 1990. Relationships between reproduction traits, age and body weight at calving, and days dry in first lactation Ayrshires and Holsteins. *Journal of Dairy Science*, 73(3): 835-842.

Morton, J., Larcombe, M., & Little, S. (Editors). 2003. *The InCalf Book for Dairy Farmers*. Australia: Dairy Australia.

Mostert, B.E., Van der Westhuizen, R.R. & Theron, H., 2010. Calving interval genetic parameters and trends for dairy breeds in south Africa. *SA J. Anim. Sci*. 40: 156-162.

Muller, C.J.C., Cloete, S.W.P., Potgieter, J.P. & Zishiri, O., 2010. Genetic parameters for fertility traits in South African Holstein cows. *Proc. 9th WCGALP*, Leipzig. Poster PP1-37. pp. 198.

Muller, C.J.C., Cloete, S.W.P., Potgieter, J.P., Botha, J.A. & G. van Pittius, Méshelle., 2006. Estimation of genetic parameters for fertility traits in Holstein cows in South Africa. SASAS Congress, 3-6 April 2006. Bloemfontein. 9.

Nebel, R.L. & Jobst, S.M., 1998. Evaluation of systematic breeding programs of lactating dairy cows: A Review. *Journal of Dairy Science*, 81(4): 1169-1174.

Norman, H.D., Miller, R.H., Vanraden, P.M. & Wright, J.R., 2002. Genetic relationships among fertility traits of Holsteins and Jerseys. *Journal Dairy Science*, 85 (Suppl. 1): 89. (Abstr.53).

Olori, V.E., Meuwissen, T.H.E. & Veerkamp, R.F., 2002. Calving interval and survival breeding values as measure of cow fertility in a pasture-based production system with seasonal calving. *Journal of Dairy Science*, 85(3): 689-696.

Oltenacu P.A., Rounsaville T.R., Milligan R.A. & Foote, R.H., 1981. Systems analysis for designing reproductive management programs to increase production and profit in dairy herds. *Journal of Dairy Science*, 64(10): 2096-2104.

Oltenacu, P.A., Frick, A. & Lindhé, B., 1991. Relationship of fertility to milk yield in Swedish cattle. *Journal of Dairy Science*, 74(1): 264-268.

Oltenacu, P.A., & Algers, B., 2005. Selection for increased production and the welfare of dairy cows: are new breeding goals needed? *Ambio*, 34(4-5): 311–315.

Oseni, S., Tsuruta, S., Misztal, I., & Rekaya, R., 2004. Genetic parameters for days open and pregnancy rates in US Holsteins using different editing criteria. *Journal of Dairy Science*, 87(12): 4327–4333.

Philipsson, J., 1981. Genetic aspects of female fertility in dairy cattle. *Livestock Production Science*, 8(4): 307-319.

Potgieter, J.P., Muller, C.J.C., Cloete, S.W.P. & Botha, J.A., 2004. Heritability estimates of fertility parameters in two Jersey herds. 2nd Joint Congress of GSSA and SASAS. 28 June-1 July 2004. Goudini. p. 121.

Pryce, J.E., Veerkamp, R.F., Thompson, R., Hill, W.G. & Simm, G., 1997. Genetic aspects of common health disorders and measures of fertility in Holstein-Friesian dairy cattle. *Animal Science*, 65: 353-360.

Pryce, J.E., Nielsen, B.L., Veerkamp, R.F. & Simm, G., 1999. Genotype and feeding system effects and interactions for health and fertility traits in dairy cattle. *Livestock Production Science*, 57(3): 193-201.

Pryce, J.E. & Veerkamp, R.F., 2001. The incorporation of fertility indices in genetic improvement programmes. British Society for Animal Science. Occasional Publication Vol. 26: 237-250.

Pryce, J.E., Coffey, M.P. & Simm, G., 2001. The relationship between body condition score and reproductive performance. *Journal of Dairy Science*, 84(6): 1508-1515.

Pryce, J.E., Simm, G. & Robinson, J., 2002. Effects of selection for production and maternal diet on maiden heifer fertility. *Animal Science*, 74(3): 415-421.

Pryce, J.E., Royal, M.D., Garnsworthy, P.C. & Mao, I.L., 2004. Fertility in high-producing dairy cows. *Livestock Production Science*, 86(1-3): 125-135.

Pursley, J.R., Kosorok, M.R. & Wiltbank, M.C., 1997. Reproductive management of lactating dairy cows using synchronization of ovulation. *Journal of Dairy Science* 80(2): 301-306.

Pursley, J.R., Wiltbank, M.C., Stevenson, J.S., Ottobre, J.S., Garverick, H.A. & Anderson, L.L., 1997. Pregnancy rates per artificial insemination for cows and heifers inseminated at a synchronized ovulation or synchronized estrus. *Journal of Dairy Science*, 80(2): 295-300.

Raheja, K.L., Burnside, E.B. & Schaeffer, L.R., 1989. Relationships between fertility and production in Holstein dairy cattle in different lactations. *Journal of Dairy Science*, 72(10): 2670-2678.

Raheja, K.L., Nadarajah, L. & Burnside, E.B., 1989. Relationship of bull fertility with daughter fertility and production traits in Holstein dairy cattle. *Journal of Dairy Science*, 72(10): 2679-2682.

Raizman, E.A., Santos, J.E. & Thurmond, M.C., 2002. The effect of left displacement of abomasum corrected by toggle-pin suture on lactation, reproduction, and health of Holstein dairy cows. *Journal of Dairy Science* 85(5): 1157-1164.

Rajala-Schultz, P.J. & Frazer, G.S., 2003. Reproductive performance in Ohio dairy herds in the 1990s. *Animal Reproduction Science*, 76:127-142.

Roxstrom, A., Strandberg, E., Berglund, B., Emanuelson, U. & Philipsson, J., 2001. Genetic and environmental correlations among female fertility traits and milk production in different parities of Swedish Red and White dairy cattle. *Acta Agriculturae Scandinavica. Section A Animal Science* 51: 7-14.

Roxstrom, A. & Strandberg, E., 2002. Genetic analysis of functional, fertility-, mastitis-, and production-determined length of productive life in Swedish dairy cattle. *Livestock Production Science*, 74:125-135.

Royal, M.D., Darwash, A.O., Flint, A.P.F., Webb, R., Woolliams, J.A. & Lamming, G.E., 2000. Declining fertility in dairy cattle: changes in traditional and endocrine parameters of fertility. *Animal Science*, 70: 487-501.

Royal, M.D., Mann, G.E. & Flint, A.P.F., 2000. Strategies for reversing the trend towards subfertility in dairy cattle. *Veterinary Journal*,160(1): 53-60.

Royal, M.D., Woolliams, J.A., Webb, R. & Flint, A.P.F., 2000. Estimation of genetic variation in the interval from parturition to commencement of luteal activity in Holstein – Friesian dairy cows. *Proceedings of the Journal of Reproduction and Fertility*, Series 25: Abstract 74.

Royal, M.D., Darwash, A.O., Flint, A.P.F., Webb, R., Woolliams, J.A. & Lamming, G.E., 2000. Declining fertility in dairy cattle: changes in traditional and endocrine parameters of fertility. *Animal Science*, 70: 487-501.

Royal, M.D., Flint, A.P.F. & Woolliams, J.A., 2002. Genetic and phenotypic relationships among endocrine and traditional fertility traits and production traits in Holstein–Friesian dairy cows. *Journal of Dairy Science*, 85(4):958–67.

Royal, M.D., Pryce, J.E., Woolliams, J.A. & Flint, A.P.F., 2002. The genetic relationship between commencement of luteal activity and calving interval, body condition score, production and linear type traits in Holstein – Friesian dairy cattle. *Journal of Dairy Science*, 85(11): 3071-3080.

Schaeffer, L.R., 1984. Sire and cow evaluation under multiple trait models. *Journal of Dairy Science*, 67: 1567-1580.

Sorensen, D.A. & Gianola, D., 2002. Likelihood, Bayesian, and MCMC methods in quantative genetics. Springer-Verlag. New York, NY.

Starbuck, M.J., Dailey, R.A. & Inskeep, E.K., 2004. Factors affecting retention of early pregnancy in dairy cattle. *Animal Reproduction Science*, 84(1-2): 27-39.

Stevenson, J.S., 2001. Reproductive management of dairy cows in high milk producing herds. *Journal of Dairy Science*, 84(E. Supplement): E128-E143.

Stott, A.W., Veerkamp, R.F. & Wassell, T.R., 1999. The economics of fertility in the dairy herd. *Animal Science*, 68: 49-58.

Taylor, J.F., Everett, R.W. & Bean, B., 1985. Systematic environmental, direct, and service sire effects on conception rate in artificially inseminated Holstein cows. *Journal of Dairy Science*, 68(11): 3004-3022.

Tempelman, R.J. & Gianola, D., 1996. A mixed effects model for over dispersed count data in animal breeding. *Biometrics*, 52: 265-279.

Thaller, G., 1997. Genetics and breeding for fertility. *Interbull Bulletin*. No 18, 55-61.

Uchida, K., Mandebvu, P., Ballard, C.S., Sniffen, C.J. & Carter, M.P., 2001. Effect of feeding a combination of zinc, manganese and copper amino acid complexes, and cobalt glucoheptonate on performance of early lactation high producing dairy cows. *Animal Feed Science and Technology,* 93: 193-203.

Van Doormaal, B.J., Kistemaker, G., Fatchi, J., Miglior, F., Jamrozik, J. & Schaeffer, L.R., 2004. Genetic evaluation of female fertility in Canadian dairy breeds. *Interbull Bull*. 32: 86-89.

VanRaden, P.M & Tooker, M., 2003. Definition of traits and comparison of models for genetic evaluation of cow fertility. *Journal of Dairy Science,* 86 (Suppl. 1): 131 (Abstr.520).

VanRaden, P.M., Sanders, A.H., Tooker, M.E., Miller, R.H., Norman, H.D., Kuhn, M.T. & Wiggans, G.R., 2004. Development of a national genetic evaluation for cow fertility. *Journal of Dairy Science*, 87(7): 2285–2292.

Veerkamp, R.F., Oldenbroek, J.K., Van Der Lende, T., 1997. The use of milk progesterone measurements for genetic improvement of fertility traits in dairy cattle. Proceedings International Workshop on Genetic Improvement of Functional Traits in Cattle; Fertility and Reproduction, GRUB, Germany, November 23-25, Vol. 18. Interbull, pp. 62 – 65.

Veerkamp, R.F., Oldenbroek, J.K., Van der Gaast, H.J. & Van der Werf, J.H.J., 2000. Genetic correlation between days until start of luteal activity and milk yield, energy balance and live weights. *Journal of Dairy Science,* 83(3): 577–583.

Veerkamp, R.F., Koenen, E.P.C. & De Jong, G., 2001. Genetic correlations among body condition score, yield, and fertility in first-parity cows estimated by random regression models. *Journal of Dairy Science,* 84(10): 2327-2335.

Veerkamp, R.F., Beerda, B. & Van der Lende, T., 2003. Effects of genetic selection for milk yield on energy balance, levels of hormones, and metabolites in lactating cattle, and possible links to reduced fertility's. *Livestock Production Science,* 83: 257-275.

Walker, W.L., Nebel, R.L. & McGilliard, M.L., 1996. Time of ovulation relative to mounting activity in dairy cattle. *Journal of Dairy Science*, 79(9): 1555-1561.

Wall, E., Brotherstone, S., Woolliams, J.A., Banos, G. & Coffey, M.P., 2003. Genetic evaluation of fertility using direct and correlated traits. *Journal of Dairy Science*, 86(12): 4093-4102.

Wathes, D.C. & Wooding, F.B.P., 1980. An electron microscopic study of implantation in the cow. *American Journal of Anatomy*, 159: 285-306.

Webb, R., Gong, J.G. & Bramley, T.A., 1992. Role of growth hormone and intrafollicular peptides in follicle development in cattle. *Theriogenology*, 41: 25-30.

Webb, R., Gong, J.G., Law, A.S. & Rusbridge, S.M., 1994. Control of ovarian function in cattle. *Journal of Reproduction and Fertility*, Suppl. 45: 141-156.

Webb, R., Royal, M.D., Gong, J.G. & Garnsworthy, P.C., 1999. The influence of nutrition on fertility. *Cattle Practice*, 7(3): 198 - 202

Weigel, K.A., 2006. Prospects for improving reproductive performance through genetic selection. *Animal Reproduction Science*, 96: 323-328.

Weigel, K.A., 2000. Toward national fertility evaluations. Proc 18th Technical Conference on Artificial Insemination and Reproduction.

Weigel, K.A. & Rekaya, R., 2000. Genetic parameters for reproductive traits of Holstein cattle in California and Minnesota. *Journal of Dairy Science,* 83(5): 1072-1080.

Weller, J.I., 1989. Genetic analysis of fertility traits in Israeli dairy cattle. *Journal of Dairy Science*, 72(10): 2644-2650.

Weller, J.I. & Folman, Y., 1990. Effects of calf value and reproductive management on optimum days to first breeding. *Journal of Dairy Science*, 73: 1318-1326.

Weller J.I. & Ron, M., 1992. Genetic analysis of fertility traits in Israeli Holsteins by linear and threshold models. *Journal of Dairy Science*, 75: 2541-2548.

Westwood, C.T., Lean, I.J, Garvin, J.K. & Wynn, P.C., 2000. Effects of genetic merit and varyaing protein degradability on lactating dairy cows. *Journal of Dairy Science*, 83(12): 2926 – 2940.

Windig, J.J., Calus, M.P.L. & Veerkamp, R.F., 2005. Influence of herd environment on health and fertility and their relationship with milk production. *Journal of Dairy Science*, 88(1): 335–347.

Windig, J.J., Calus, M.P.L., Beerda, B. & Veerkamp, R.F., 2006. Genetic correlations between milk production and health and fertility depending on herd environment. *Journal of Dairy Science*, 89(5): 1765–1775.

.

Wolfenson, D., Roth, Z. & Meidan, R., 2000. Impaired reproduction in heat-stressed cattle: basic and applied aspects. *Animal Reproduction Science*, 60-61: 535-547.